ASPECTS OF SCIENCE
IN
WESTERN AUSTRALIA

1829

1979

A volume to commemorate the 150th Anniversary of the founding of Western Australia

Journal of the Royal Society of Western Australia, Vol. 62, Parts 1-4, 1979.

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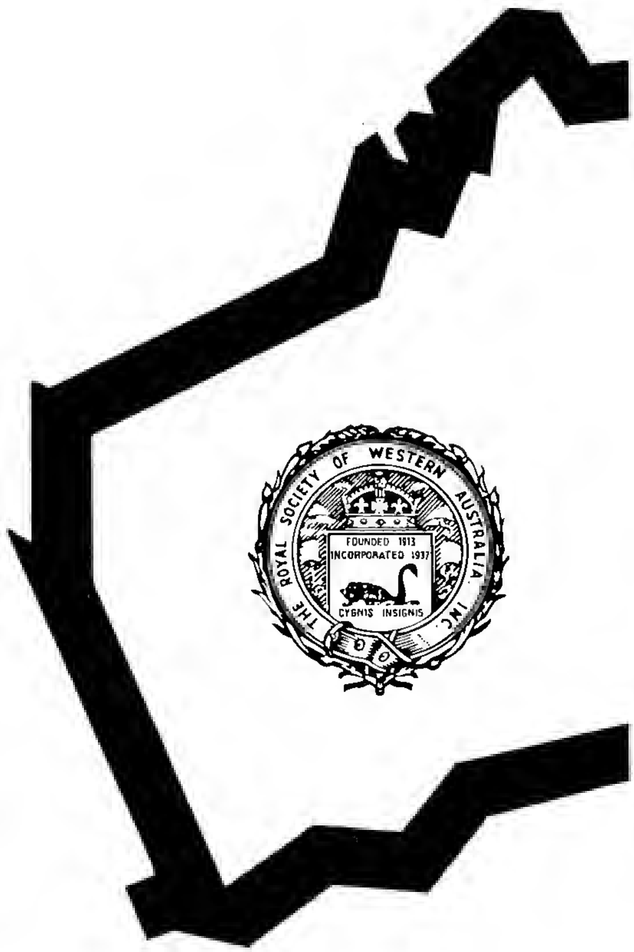

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ASPECTS OF SCIENCE IN WESTERN AUSTRALIA

Preface

When the early settlers landed in Western Australia in 1829 their first priority was to wrest a living from the new and often hostile environment. They had little inclination or opportunity to study the unique flora and fauna which surrounded them and gave the bush creatures such misleading and unimaginative names as native cat, native squirrel and native porcupine and the commonest black and white bird was dubbed a magpie.

However, as more and more new plants and animals were found by explorers and collectors popular interest was kindled and by 1891 the Premier Sir John Forrest sponsored the formation of the Western Australian Natural History Society.

This Society was short lived and became defunct in 1895, but again with impetus from Sir John Forrest it was succeeded in 1897 by the Mueller Botanical Society which was later expanded to embrace all forms of natural history and laid the foundations for the Royal Society of Western Australia.

Since receiving its official Charter in December 1913 the Royal Society has been very careful to comply with section two of its constitution—

"To promote and assist in the advancement of science."

The 61 volumes of the *Journal of the Royal Society of Western Australia* so far published cover a wide range of scientific disciplines and have earned for the Society a very high reputation amongst scientists in many parts of the world.

In presenting a special publication to commemorate the 150th Anniversary of the Founding of Western Australia the Royal Society is proud of the fact that many of its members have played an important part in the development of the State and that some of the most important research findings first appeared in its Journal.

The Society is grateful to the State Government for supporting its work in past years and looks forward to the day when it will celebrate its own 150th anniversary.

C. F. H. Jenkins,
President.

Journal of the Royal Society of Western Australia, Vol. 62, Parts 1-4, 1979, p. 3-11.

Aspects of Science in Western Australia 1829-1979.
A volume to commemorate the 150th Anniversary of the founding of Western Australia.

History of geology in Western Australia

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Abstract

Geology was of great interest to the early settlers because they realized that, if their new colony was ever to develop rapidly, something in addition to agriculture was required; hence the interest in locating economic mineral deposits. In the first 70 years geology was practised mainly by explorers and rarely by professional geologists, which the colony could only occasionally afford to employ. This situation changed with the first major mineral discovery—gold. Each major economic advance in Western Australia has stemmed from new mineral discoveries. This has resulted in the expansion of interest in and development of geology in government, academic and industrial fields.

The beginning

In the development of Western Australia during the past 150 years all of the periods of major economic growth can be related to mineral discoveries. Geology has therefore played a major role in this development. Most of the original settlers came with expectations of a fertile land from which their own requirements could be met by agriculture and animal husbandry, but they soon realized that, apart from relatively small areas such as along the Swan and Greenough River valleys, the land was poor and their methods yielded a bare subsistence. Obviously something more was required to attract new settlers and to provide earnings to finance roads, schools, hospitals, harbours and other essential public works.

Fortunately among the settlers were men of vision who were prepared to look further afield, and who became explorers; together with the early surveyors, they ventured into the unknown interior in search of better prospects. While these persons were not trained geologists, they were in many cases very good observers and recorded the nature of the ground they traversed. Also, because of the struggle for survival in these early years, a few appreciated the advantages which would accrue to the young colony if economic minerals were discovered. As early as 1839 the Government offered a free grant of 1 036 hectares of land to the first person to discover a coal seam. Later a German naturalist, Preiss, reported finding coal on the Murray River. Specimens of this poor quality coal raised hopes, and rumours of the mineral potential of the colony were spread.

In September 1846, a prospectus to form a company (The Western Australian Mining Company) with a capital of $40 000 was issued. This, and the persistent rumours, generated the first mineral boom for this State. To add to the enthusiasm A. C. Gregory, the Assistant Surveyor General, and his brothers, F. T. and H. C. Gregory, reported the discovery of coal on the Irwin River on 9 September 1846 and claimed the free grant of land for the first discovery of coal.

The company commenced drilling near the Murray River and reached a depth of 12 m encountering some coal of doubtful quality. Through inexperience and shareholders who, (like those of today) were looking for quick returns, the company was soon in difficulties. In order to assess the potential, the company engaged Dr Ferdinand von Sommer, variously described as "mining expert", "eminent mineralogist", or "geologist". His remuneration was £6 per month with keep which amounted to £12 19s 2d per month at Leeders Hotel and the company horse. von Sommer arrived from Adelaide on 15 February 1847, accompanied by an experienced miner named Thomas.

The company was also interested in possible lead or copper deposits between the Canning and Serpentine Rivers, but the investigation for both coal and metallic minerals was unsuccessful. von Sommer's employment with the Western Australian Mining Company had lasted only a few months. In mid-1847 he was commissioned by the Governor to accompany the Surveyor General to examine the Gregory brothers' coal find on the Irwin River. It appears that von Sommer was the first professional geologist to work in Western Australia and the first employed by the Government. He travelled extensively for those days, examining the Victoria, Toodyay and York districts, the country between York and Mount Barren and the area from Doubtful Island Bay to Cape Naturaliste.

According to records this work was done in 1847 and 1848 and von Sommer wrote four reports to the Colonial Secretary which are

recorded in exploration diaries of the Lands Department. He contributed three papers to the geological literature of the day and three original drawings of his geological observations are preserved by the Geological Survey as the first known geological maps of Western Australia. von Sommer's later activities are unknown, and he left the colony in 1851.

The Gregory brothers, particularly A. C. and F. T., both of whom were in the department of the Surveyor General, carried out jointly and separately many exploratory expeditions between 1846 and 1862, first in southern Western Australia, then in the North-West, and later across northern Australia. They were keen observers and their records frequently describe the geology of the area over which they travelled. They had a good knowledge of geology and contributed papers to the Royal Geographical Society, of which they were Fellows.

In 1848 F. T. Gregory discovered lead and some copper in the bed of the Murchison River and this occurrence, named Geraldine, became the first lead mine in Western Australia. After an extensive exploration trip through the North-West, he reported "of mineral I was unable to discover any traces, except iron". A geological map of the colony by the Gregorys was published in London in 1860.

Due to the financial difficulties experienced by the young colony, it was not until 1870 that it was again possible to engage a geologist, namely H. Y. Lyle Brown. It would appear that he was given a two-year contract to report on the geology of the colony, as then settled or known. In his period of service Brown prepared three maps and ten reports on the areas he examined, which extended from the Murchison southwards along the coast to Doubtful Island Bay, and inland to the extent of the settled area. A geological map of this area was published on a scale of about 18 miles to an inch. He later became the Government Geologist of South Australia (1882-1912).

In April 1870, a clergyman/scholar the Reverend Charles Grenfell Nicolay arrived in Western Australia. He was a man of many parts with the ability to antagonize some people and please others. Nicolay, who was a Fellow of the Royal Geographical Society, had been associated with the King's and Queen's (now defunct) Colleges in London, having been largely responsible for founding the latter, where he was Professor of Geography and Ancient History. In Western Australia he apparently impressed the Governors of the day, and, besides his church duties, he became an adviser to the Government (1881-1889) on technical and scientific matters. His contributions to geology included an investigation of a ship canal from the sea to Rocky Bay on the Swan River to develop a major harbour at Fremantle (probably the first engineering geology done in this State), an investigation of the reports of coal in the bed of the Fitzgerald River, a "Handbook of Western Australia" (1881), the geology of the railway route between Guildford and Clackline (1887) and a circular on prospecting for gold (1886). He also prepared a rock and mineral collection together with some notes on the geology of Western Australia for the Colonial and Indian Exhibition of 1886, a contribution to a commission enquiring into the water supply of Perth and Fremantle, and identifications of rocks and minerals. In 1881 he was authorized by Governor Robinson to establish at Fremantle a collection of rocks and minerals of the colony. Nicolay continued his many and varied interests in the colony until his death in 1897 at the age of 81.

After the departure of H. Y. Lyle Brown it was nine years before the colony could afford to employ a geologist again. E. G. Hardman of the Geological Survey of Ireland was appointed in 1882 and stayed until 1885 when the colony again could no longer afford the services of a geologist. Hardman concentrated his efforts on the Kimberley region and published two major reports on his field work. These stimulated the search for gold in this area, resulting in the first find of gold in the colony by Hall and party in 1885. The Government had offered a reward of $20 000 to the discoverer of the first goldfield to produce 10 000 ounces. While the Kimberley find did not produce the required amount of gold, the Government paid $1 000 reward each to Hardman and Hall. Hardman also examined and reported on the geology of the Bunbury and Blackwood River areas and on the water supply of Perth and Fremantle.

Hardman made a major contribution to the early geology of the State and returned to Ireland with an assurance that he would become Government Geologist when the Government could afford to make a permanent appointment. Unfortunately he died early in 1887, the year in which it was decided to make such an appointment.

H. P. Woodward, who had been Assistant Geologist to H. Y. Lyle Brown in South Australia, was appointed Government Geologist for a term of five years and commenced duty in January 1888. He had B. H. Woodward appointed as assayer and curator of the Geological Museum, while in 1894 S. Göczel was appointed as Field Geologist and Mining Engineer.

This was a very exciting period for Western Australia with gold discoveries being made progressively throughout the colony, commencing in the Kimberley in 1885 and culminating with Kalgoorlie in 1894. Woodward covered large areas of Western Australia and produced short reports on his observations for the Government. His major work was probably the Mining Handbook issued in 1894 with a second edition in 1895. This volume, 216 pages with maps, must have been extremely useful at that time because as well as a description of the physiography and geology, it contained a wealth of other information including the known mineral occurrences and resources, general information for prospectors, and shipping, railway, postal and telegraph information. Another accomplishment of Woodward was the first coloured geological map of the State published in 1894 by the Government.

The colony began to appreciate the value of competent geological advice through the efforts of Brown, Hardman and Woodward, particularly with the discovery of gold, which caused the first major development. Woodward's contract was extended to the end of 1895 when he resigned, as did his two assistants. Apparently there were better-paid positions available elsewhere in private enterprise. This resulted in a firm decision being made to establish a permanent Geological Survey in this State.

Until this period the knowledge and development of geology had been confined to the occasional Government Geologist employed by the colony and to dedicated explorers or surveyors, who had acquired a knowledge of geology by reading and experience. From this time geology was to be developed in Western Australia by three groups of geologists: those associated with Government Geological Surveys; the teachers and research workers in educational institutions; and consultants or geologists employed by companies.

Government geological surveys

Andrew Gibb Maitland was appointed as Government Geologist in charge of the first permanent State Geological Survey. He started work in November 1896 and established an office with a staff of nine, including three geologists, a mineralogist, a topographic surveyor, a draftsman, a laboratory assistant, a cadet and a clerk/accountant.

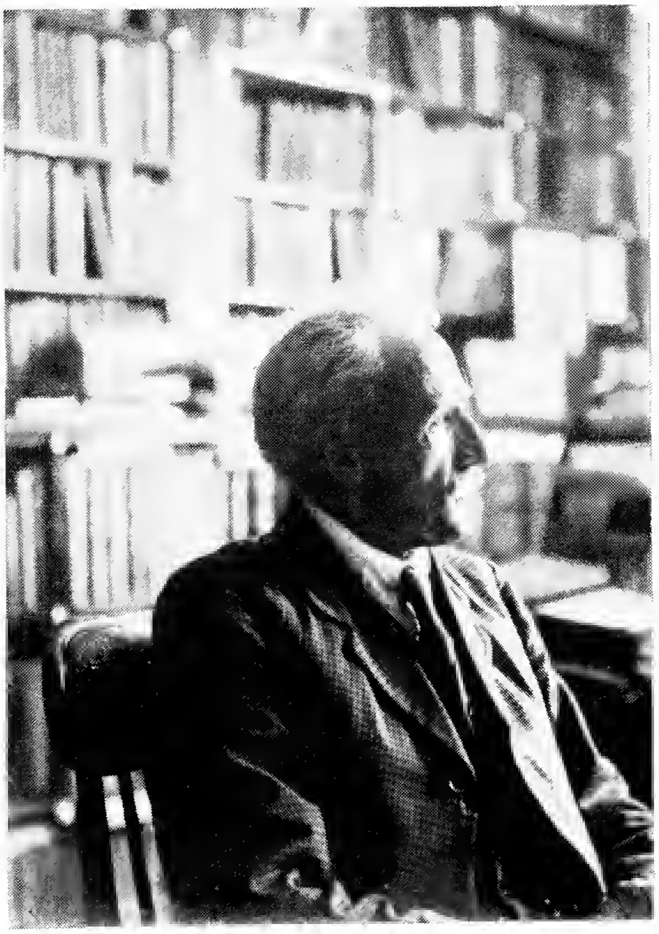

Figure 1.—Andrew Gibb Maitland, the first Government Geologist in charge of a permanent Geological Survey.

By 1912 the professional staff had increased to ten; but later it decreased, until during the 1930s it averaged only three. It did not rise to ten again until 1959. From 1961 onwards a major expansion was approved and the number of staff grew rapidly until at the end of 1978 the establishment was 63 professional officers. The Government Geologists (now titled Director) in charge over this period were: Andrew Gibb Maitland (1896-1926, Fig. 1); Torrington Blatchford (1926-1934); Frank G. Forman (1934-1944); H. A. (Matt) Ellis (1945-1961), and J. H. (Joe) Lord (1961-present).

Until 1961 the geologists practised in all fields of geology, with emphasis on geological mapping and examination of mineral resources. It was excellent general training for geologists, but without opportunity to specialize in any particular field. After the expansion in 1961, geologists were recruited for their particular experience or training in specific fields of geology. The Survey now has divisions covering most facets of geology, namely hydrogeology (13 geologists), engineering geology (4), mineral resources (9), regional geology (9), sedimentary geology (9) and sections in petrology (3), palaeontology (3), geophysics (2), geochemistry (1), environmental geology (2) and technical information (4).

Following the 1961 expansion of the Geological Survey special emphasis has been placed on regional geological mapping to ensure that the geology of the whole State is mapped at the useful 1:250 000 scale. The field work for the last of the 163 maps should be completed in this 150th Anniversary year. In this arid State hydrogeology has become a major function of the Survey in the search for groundwater for town supplies, mining operations, and for farmers and pastoralists. In the future more detailed geological mapping is proposed for areas covering mineralized belts.

Over the last 18 years, while efforts have been mainly directed towards systematic geological mapping, the Survey may have lost close contact with the prospector and exploration companies in the field, but this was necessary if the mapping were to be done in a reasonable time. To help restore this contact it is now intended to open regional offices at several major country centres.

The Commonwealth Government first became involved in the geology of this State with the passing of the Northern Australian Survey Act of 1934, which gave authority to establish the Aerial, Geological and Geophysical Survey of Northern Australia (AGGSNA). The first meetings of this organization were held in June 1934 and field parties started work in April 1935. AGGSNA consisted of the Commonwealth (Northern Territory), Queensland and Western Australia, who agreed to start the three year programme of work in each region north of 22°S latitude. The Commonwealth contributed $150 000 and each State $75 000 to search for

metallic minerals, particularly gold. A geological party was established in each State and two geophysical parties which investigated problems as and where required. The programme in Western Australia extended beyond the planned three years with field work being completed in 1938. The unit was disbanded in June 1939.

Some 64 reports on the Western Australian work were published. The young geologists involved in AGGSNA were later to become leaders in the profession. Dr W. G. Woolnough was the Commonwealth geological advisor for the creation of AGGSNA and there is little doubt that his enthusiasm was largely responsible for the Commonwealth Government establishing the Bureau of Mineral Resources (BMR) immediately after World War II

The BMR has been a major contributor to the geology of this State, particularly prior to the expansion of the Survey. Earlier the BMR carried out all geological mapping in the sedimentary basins while in more recent years it has contributed to joint mapping parties. In the field of geophysics the BMR has been particularly active with regional aeromagnetic and gravity surveys.

Educational institutions

As interest in geology heightened with the gold discoveries of the 1890s, a demand arose for the subject to be taught at the limited educational facilities available at that time. In 1900 Perth Technical School offered courses in geology and mineralogy and these were probably the first formal classes established. The lecturer was F. C. Stockwell.

The School of Mines of Western Australia, under the control of the Department of Mines, was opened at Coolgardie in November 1902, and then was moved to Kalgoorlie at the end of 1903. Geology and mineralogy were amongst the first courses offered. The School of Mines, because of its locality, became a centre for mining geology, although it was not until 1947 that a full associateship course was established.

The lecturer who probably deserves most recognition is Dr C. O. G. Larcombe, who joined the School in 1907 and remained there until early 1934. He was responsible for planning the Mineral Museum which opened on 7 December 1907, and is a feature of the School of Mines today. Larcombe was particularly interested in petrology and mineralogy, and he also acted as petrologist to the Geological Survey of Western Australia from 1922 to 1928. His best known publication was "The Geology of Kalgoorlie with Special Reference to the Ore Body" published in 1911 by the Australasian Institute of Mining Engineers.

The School has always maintained an active interest in the geology of the Kalgoorlie area. Larcombe contributed many papers on this topic, while Dr F. L. Stillwell, on loan from the Commonwealth Scientific and Industrial Research (CSIR), used the School as a base for his study in 1927 and 1928 of the "Geology and Ore Deposits of the Boulder Belt, Kalgoorlie" published as Geological Survey Bulletin 94. In later years G. S. Compton and W. H. Cleverly were in charge of the geology department. When the Western Australian Institute of Technology (WAIT) took control of the School of Mines at Kalgoorlie in 1969 the Geology Departments of the two establishments were amalgamated, with the head of the Geology Department being at WAIT near Perth.

WAIT was established in 1967 with an associateship course in geology. This course, which was upgraded to a degree course in 1975, is designed to educate in the practical aspects of geology, but there has been insufficient time as yet for the graduates to make their mark.

When a university was first founded in this State, limited finance restricted its scope to the establishment of only seven chairs, exclusive of Agriculture which was endowed. There was much discussion and lobbying as to which disciplines should be represented. The first six decided upon were Mathematics and Physics, Mining (now dropped) and Engineering, Biology, History and Economics, English, Chemistry, leaving the seventh chair to be either Classics, Education or Geology. Voting was eventually deadlocked between Classics and Geology, leaving the Chancellor, Sir Winthrop Hackett, a well known supporter of the Classics, with the casting vote. To the Senate's surprise the Chancellor gave his vote to Geology because of the importance of the mining industry to this State, a fact which was realized in 1912 but is often overlooked today.

By the time the University opened in 1913, Walter George Woolnough (Fig. 2) had been appointed the first Professor of Geology at the University of Western Australia. He had studied at the University of Sydney under the father of geology in Australia, Professor Sir Edgeworth David, and had gained the first D.Sc. awarded by that University. He travelled extensively in Australia and Fiji and had lectured at the Universities of Sydney and Adelaide. As the first geology professor in this State he was an excellent choice, being a lucid lecturer and devoted to his students to whom he gave a good grounding in practical geology.

He resigned in 1919 and worked on economic mineral deposits in all areas of Australia. In 1927 he was appointed Geological Adviser to the Commonwealth Government, a position he was reluctant to leave on reaching retirement age in 1941, having laid the foundations for the development of the Bureau of Mineral Resources. He pioneered the use of aerial photography for geological purposes in Australia, gave close attention to the oil possibilities of the north west of this State, in particular the Exmouth Gulf area, and was responsible for the investigation of Yampi Sound iron ore deposits.

The Geology Department of the University had been given a solid foundation by Woolnough, but on his resignation it was decided, due to the shortage of finance, to abolish the chair and to appoint a lecturer-in-charge instead. This

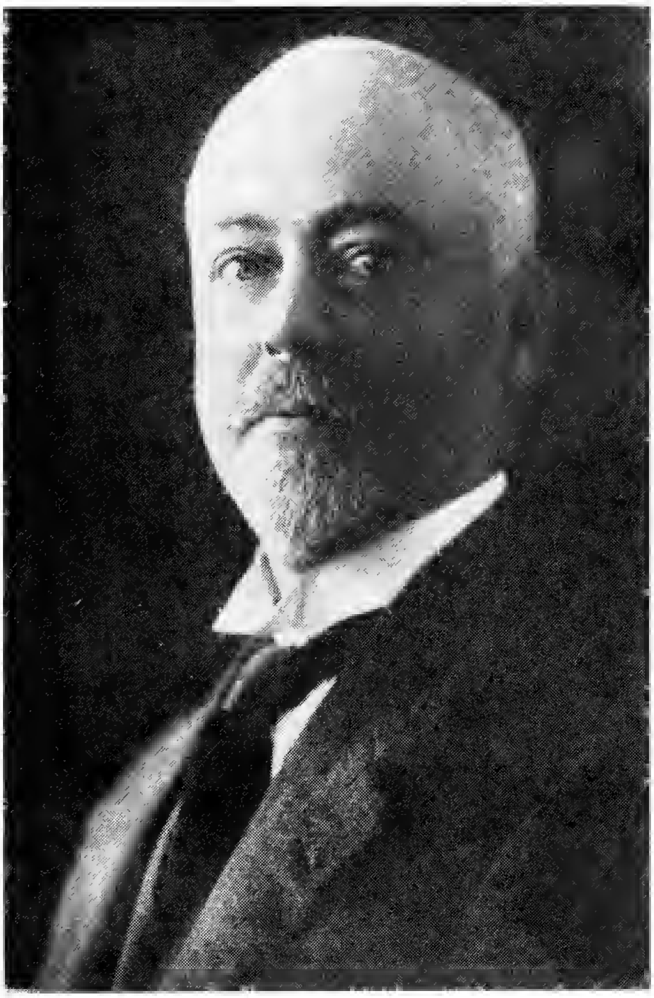

Figure 2.—Walter George Woolnough, the first professor of geology at the University of Western Australia.

decision allowed the estimated expenditure for the geology department to be reduced from $3 176 in 1919 to $1 080 in 1920.

Edward de Courcy Clarke was appointed to the position of Lecturer but did not commence duty until 1921. He was a graduate of University College, Auckland, and had joined the Geological Survey of Western Australia in 1912 as a field geologist. He travelled extensively in Western Australia and produced six bulletins regarding his investigations on the goldfields, and had made a reconnaissance survey with H. W. B. Talbot of the country between Laverton and the South Australian border. He enjoyed field work and practical geology, spending 356 days in the field around Meekatharra in 1914.

As a lecturer his enthusiasm for practical geology was always evident and he was a worthy successor to Woolnough. In 1930 the chair of geology was re-established; Clarke was appointed and occupied it until his retirement in 1948. He was a dedicated man with simple tastes and an ability to encourage and inspire his students, whose interests he placed above all others. He consolidated the Geology Department and established its reputation. His main interest was Precambrian geology, although in the latter part of his career he was co-author with his staff of many papers on the geology of younger rocks.

Clarke was succeeded by one of his outstanding students, Rex T. Prider, who carried on the traditions established by Clarke until he retired in 1975. Peter G. Harris, another New Zealand graduate, now occupies the chair.

During the past 30 years the Geology Department has gradually expanded to meet the demand for more geologists and research. One might expect that this Department of the major University in Western Australia would, because of the huge mineral wealth in the State, have developed into a major centre for research into the Precambrian rocks and mineral deposits. This has not eventuated although such centres have now developed in other Australian Universities.

Consulting and company geology

The discovery of the Golden Mile near Kalgoorlie in 1894 created world-wide interest in Western Australia, resulting in visits by overseas consulting geologists and mining engineers, as well as government and academic geologists. Many of these persons wrote of their observations and opinions. Amongst those who published papers within the first ten years of the discovery were: G. J. Bancroft, H. Y. L. Brown, Y. F. Bulman, A. F. Calvert, S. W. Tard, A. Carnot, A. G. Charlton, C. Chewings, H. B. Corbin, William Frenchville, E. Halse, H. G. Holroyd, Herbert C. Hoover, J. F. Kemp, P. M. Krause, P. Krusch, Baron Sloet van Oldriutenburgh, E. F. Pitman, T. A. Rickard, Bergrath Schmeisner and Brenton-Symons. After the initial flurry, from about 1910 onwards more detailed geological examinations were made by consultants, who stayed longer. Many of their reports were no doubt confidential to the companies concerned. Amongst these were Dr Malcolm McLaren (representing the London Mining House, Gold Fields), Dr J. A. Thomson, R. Lockhart Jack and T. Esdaile.

Due to World War I and the depressed conditions for gold in the aftermath, little work is recorded by private consultants or companies in this period. In 1928 Malcolm McLaren returned to look at the Lake View and Star Mine at Kalgoorlie and the Moonlight-Wiluna Gold mine at Wiluna. Probably through him a Geological Section was established at the Lake View and Star Mine in 1929 with a young geologist from Canada, R. F. Playter, in charge, assisted by Harold Jensen. This was probably the first company geological office established in this State.

In 1933 Western Mining Corporation (WMC) was formed by William Sydney Robinson, who was a strong supporter and instigator of a scientific approach to exploration. This has certainly been proved profitable when one looks at WMC's existing mines and prospects (Yeelirrie, Roxby Downs and Benambra). A Geological Department was established with J. D. Campbell, H. W. B. Talbot, A. Blatchford and K. J. Finucane as the first geologists.

Robinson then engaged D. McLaughlin, Professor of Economic Geology at Harvard, as consultant to the company to introduce modern methods of exploration, which he had developed, into Western Australia. McLaughlin assembled a large group of geologists who had trained under him at Harvard. H. E. McKinstry, G. K. Gustafson and F. Miller were consultants for the company from 1934 until 1936, while H. J. C. Connolly was appointed chief geologist and Haddon F. King, Frank A. Moss and R. F. Thyer joined as permanent staff members. This probably still remains the most talented group of geologists ever assembled for mineral exploration in Australia and WMC retained more geologists than any other company operating elsewhere in Australia at that time.

WMC was the first organization to apply aerial photography to mineral exploration in Australia. This technique had been suggested by South African interests in the company, and the photographic section was under the control of Wing Commander Laws, a former Royal Flying Corps pilot. Some of the experience and techniques developed were used in World War II. The group carried out factual surface mapping and interpretation. Geophysical methods were considered and ground magnetic surveys were done.

In addition, the group examined existing and former mines for extensions or repetitions. These included the southern extension of the Golden Mile, Norseman, Great Fingall (Day Dawn) and the Cosmopolitan (Kookynie). Through pursuing this policy with an active, progressive geological team, WMC has become one of Australia's major mining companies, and with such finds as mentioned earlier, it has proved that geologists as well as prospectors do find ore bodies.

After World War II, other companies such as BHP, Rio Tinto and Zinc Corporation, began to employ exploration geologists in this State and in the oil and uranium booms of the early 1950s, companies and consultants established geological departments. In the mineral boom of the 1960s and early 1970s geological sections became essential for all active companies, some of the larger companies having 60 to 80 geologists engaged at the peak of the boom.

While a number of geological consultants visited this State for varying periods, it is believed that K. J. Finucane (Fig. 3), a Western Australian graduate with wide experience, was the first to establish himself as a permanent resident consultant in 1939. He is still practising some 40 years later. In the early 1950s Frank G. Forman, a former Government Geologist, established a consultancy; he was followed by E. P. Utting and S. A. Tomich later in the decade.

The mineral boom of the 1960s saw many local and overseas individual consultants and consulting firms establish themselves in Western Australia. With the passing of the boom in 1972 some moved on, some have turned to contract work or positions with companies, while about 30 continue to practise.

Figure 3.—Kevin J. Finucane, the first resident consultant in Western Australia.

Specialized branches of geology

With the rapid development of geology in the last 2 or 3 decades many new branches or associations with geology have developed particularly in the search for minerals. These include geophysics, geochemistry, geobotany, palaeomagnetism, geochronology and others, which will eventually require a history of their own. Only the original major branches of geology are considered below.

Petrology

Petrology has a longer history in this State than any other branch of geology. This resulted from the great interest developed here and abroad with the discovery of gold at Kalgoorlie, and the necessity to unravel the petrological and structural history, a problem which is still receiving attention.

Many geologists visiting the new goldfields found great interest in the petrology and mineralogy of the telluride ores and their host rocks which led to the publication of numerous short papers while no doubt many others were held as confidential in company reports.

The first published descriptive petrology was by G. W. Carr of the Geological Survey of New South Wales on a suite of rocks from Kalgoorlie. However E. S. Simpson, although strictly a mineralogist and analyst, had joined the Geological Survey in 1897 and was contributing to petrological knowledge.

About 1910 microscopic petrology flourished with Dr J. A. Thomson, who accompanied Dr Malcolm McLaren on a lengthy consulting visit, contributing papers. Dr C. O. G. Larcombe, at the School of Mines, studied the rocks of the Golden Mile, and R. A. Farquharson joined the Survey as petrologist in 1911. After Farquharson's resignation in 1922, Larcombe acted as petrologist for the Geological Survey until 1928. The University was the next to develop petrology with the appointment of Rex T. Prider as an assistant lecturer in 1934. Later he went on to Cambridge to study for his Ph.D. and returned to the University, where he made many major contributions to the petrology of this State. The University continues to be well known for its petrological research.

Sedimentary petrology was studied at the University of Western Australia with the appointment of Dr Dorothy Carroll in 1941 as a Research Fellow. After her departure in 1943, the University did not appoint a replacement until Dr J. J. E. Glover joined as a Lecturer in 1955 and he has continued to study and teach this branch of petrology.

After Farquharson's resignation the Geological Survey did not appoint another petrologist until Dr A. F. Trendall joined the staff in 1962. The Survey's Petrology Section has now been expanded to three petrologists. Over the last 10 years joint petrological and geochronological studies with John de Laeter of WAIT have been carried out and have made a major contribution to this work in Western Australia (see de Laeter and Trendall, this volume).

Palaeontology

This branch of geology in Western Australia illustrates the development of specialization in the science. In the last century there were very few palaeontologists, but generally they examined most groups of fossils. Today, in contrast, palaeontology is a highly specialized profession, with some workers spending their lifetime studying a few genera of one particular order. This applies particularly to the study of foraminifers, due to their economic value in oil exploration.

In Western Australia the early palaeontology was of a very general nature and studied mainly by overseas workers to whom suites of specimens were sent. F. T. Gregory, over the period 1846-1861, collected fossils particularly from the Irwin and Gascoyne Rivers and Geraldton areas. The Gregory brothers made the first fossil determinations and showed the results on their geological map of 1847. Other collections of fossils were sent to England, and studied by Charles Moore, Reverend W. B. Clarke and W. H. Huddleston and reported upon in the Quarterly Journal of the Geological Society of London.

In the latter part of the 19th century E. T. Hardman and H. P. Woodward devoted some of their time as Government Geologists to the study of fossils and encouraged other specialists, such as Arthur H. Foord (brachiopoda and mollusca), R. Kidston (plant remains), H. Alleyne Nicholson (stromatoporoids) and George J. Hinde (corals and bryozoa) to become involved.

With the establishment of a permanent Geological Survey, R. Etheridge Jr., Curator and later Director of The Australian Museum, Sydney, became the honorary palaeontologist and together with others, including F. Chapman, palaeontologist, National Museum, Melbourne, and W. Howchin, palaeontologist, University of Adelaide, had numerous papers published in the Geological Survey's bulletins.

In 1908 Ludwig Glauert was engaged by the Survey as a palaeontologist, apparently the first employed full-time in this State. He prepared a catalogue of Western Australian fossils and appeared to have stimulated more work by outside specialists including E. A. Newell Arber and Rex W. Bretnall. Unfortunately Glauert resigned within two years to join the Western Australian Museum, where he continued for many years producing palaeontological papers published mainly in the Journal of the Royal Society of Western Australia.

The Geological Survey did not engage another palaeontologist until 1962; the staff of the palaeontology section has now increased to three. The palaeontologists provide general palaeontological assistance to the geological staff; palynology is particularly useful for stratigraphic control of the extensive groundwater exploratory drilling programmes carried out by the Survey.

The University of Western Australia did not specialize in palaeontology until Dr Curt Teichert was appointed a Research Fellow in 1937. During his eight years at the University, Teichert was responsible for considerable research in palaeontology and stratigraphy and his papers drew world-wide attention to this State and in particular to its oil potential. After Teichert left, the University continued to have palaeontologists on the staff, while palynology was added later to its area of research and teaching. Dr B. E. Balme, who had done an Honours thesis on palynology of the Collie coals in 1948, returned to the University some ten years later to become a Lecturer (later Reader), specializing in palynology.

In recent years the Western Australian Museum has studied vertebrate and Quaternary palaeontology.

Mineralogy

When the Geological Survey was formed provision was made for a mineralogist and assayer. In 1897 Edward S. Simpson, graduate in mining and metallurgy from the University of Sydney, was appointed to the position. He was destined to stay with the Government for 42 years and in this time made a major and oustanding contribution to his field.

As mineralogist and assayer he acted as chemist to the Department of Mines. In addition to handling work of a routine nature, he became involved in the chemistry and petrology, as well as the mineralogy, of areas being studied by the Survey. In particular he unravelled the rock types of the Golden Mile at Kalgoorlie. In 1919 he was awarded a D.Sc. from the University of Western Australia for his thesis

"The Minerals of Western Australia". Throughout his life he continued to study and accumulate information on the minerals of this State.

In 1922 he was made Government Mineralogist and analyst in charge of what is now known as the Government Chemical Laboratories, which conducts a wide variety of analytical work for numerous Government Departments. Despite these added responsibilities, he continued to promote and foster mineralogy, the study of which he retained as a major operation in the laboratories.

He published over 100 scientific papers, provided an immense amount of data for Survey publications and was working on his opus magnum summarising the mineralogical knowledge of the State when he died suddenly in August 1939, only a few months prior to retirement. His work was completed by colleagues and "Minerals of Western Australia" was eventually published in three volumes by the Government over the period 1948 to 1952. This has proved to be an invaluable reference book on the minerals of the State and their occurrence, to assist students, prospectors and exploration geologists.

Since the passing of Simpson and his immediate successors the study of mineralogy has declined. The Government Chemical Laboratories have now grown to a size where they could be decentralized to the Departments for which they work.

As mineralogy forms an integral part of petrology, geochemistry and geochronology, it continues to be studied at the University of Western Australia but there has been no strong specialization in the subject.

In 1963 the Commonwealth Scientific and Industrial Research Organization (CSIRO) opened a branch of their Division of Mineralogy in Perth. A very strong and active research section on the problems of mineralogy and mineralization in this State has been developed and is contributing to our development.

Geological museum

Rev. C. G. Nicolay, started the first collection of rocks, minerals and fossils at Fremantle in 1881. Nicolay was apparently very keen and established a good geological collection representative of the colony. To the best of his ability he tried to identify and report on the rocks and minerals that he collected or acquired. He did receive criticism from one Government Geologist of the day, E. T. Hardman, who apparently considered him to be incompetent in his identifications.

The collection assembled by Nicolay was housed at Fremantle and known as the Geological Museum. In 1889 it was transferred to Perth, to form the original collection of the Western Australian Museum.

Several collections of minerals including excellent specimens of gold and tellurides from the Kalgoorlie area were sent to exhibitions in England and Europe, but were never returned.

When Maitland formed a permanent Survey in 1896, he and his staff built up a collection of rocks and minerals. This collection far outgrew the Museum collection, and in 1908 the Government decided that the two collections, both at that time housed close together, should be amalgamated under the direction and custody of the Government Geologist, but displayed in a gallery attached to the Museum. In the amalgamated collection there were about 10 000 registered specimens of which only about 15 per cent had been derived from the Museum's collection.

The collection continued to grow until 1966 when the Museum required the gallery for other purposes and the Survey was required to remove the collection.

It was placed in store at the Survey's core and cuttings library until 1971 when Mineral House was completed with limited space for a Museum. Now nearly 1 000 specimens of Western Australian rocks, minerals and fossils are displayed in the Survey's Museum, while the remainder are still in store. The catalogue of the whole collection is now being placed on computer and retrieval of any particular specimen is relatively easy if required.

The Western Australian Museum has concentrated on a collection of vertebrate and Quaternary fossils. It also has a collection of meteorites which attracts world-wide recognition but no collection of rocks or minerals.

Conclusion

This brief review of the development of geology in the State shows that the profession has gained greater strength in the last 20 years than in the previous 130 years. This is the result of the extensive mineral development of recent times and the general acceptance that geology is necessary to locate, to explore, and to develop mineral deposits.

The growth of the profession in this State appears at first glance to be very satisfactory, until comparison is made with that of other States. In the Western Australian Geological Survey there is only one geologist per 40 000 km^2, which is the lowest density of all the Australian States. Queensland has one geologist per 24 000 km^2, while Tasmania has one per 2 100 km^2. Thus it is apparent that this situation can and should be improved as soon as finance can be made available. There is need for expansion of teaching, both at secondary and tertiary level, and research into many aspects of geology. This State should become a centre for study of both Precambrian geology (metallic minerals) and sedimentary geology (oil and gas) by the establishment of research centres, particularly in association with the tertiary institutes.

As this State, and Australia generally, depends largely upon minerals, it is the duty of the State to arrange the financing of these proposals. If this is done, our economic future will be assured and at Western Australia's bicentennial anniversary, the State will be known as a centre of geological research and geological activity, as

well as having developed into the major mineral production and processing region in Australia.

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Stromatolite research in Western Australia

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Abstract

Research on Western Australian stromatolites, both modern and ancient, has played an important role in the environmental and biostratigraphic interpretation of these enigmatic organosedimentary structures. This research has been concentrated on modern stromatolites from Hamelin Pool, Devonian stromatolites from the Canning Basin, and Proterozoic stromatolites from several areas of the State.

The first research on the Hamelin Pool stromatolites indicated that they are restricted to the intertidal zone, their morphology is controlled by environmental rather than biological factors, and they are formed solely by the trapping and binding of sedimentary particles by algal filaments. Using uniformitarian principles these conclusions were widely applied to ancient stromatolites, and as a corollary, many palaeontologists and stratigraphers concluded that stromatolites can be of no value for biostratigraphic correlation. However, each of these conclusions has subsequently been disproved or substantially modified.

Recent work at Hamelin Pool has now shown that living stromatolites there are not restricted to the intertidal zone as had previously been supposed; they grow to depths of at least 3.5 m. Indeed the subtidal occurrences are more widespread than those in the intertidal zone. Moreover, although the external morphology of stromatolites at Hamelin Pool is governed by environmental factors, their internal fabric is biologically controlled.

Stromatolites in the Devonian reef complexes of the Canning Basin grew through a wide depth range, from the intertidal zone to depths which probably exceeded 100 m. These stromatolites were not formed solely by enmeshing of clastic particles by algal filaments; biochemical precipitation of carbonate by algae and/or bacteria was also important, and was the only growth mechanism in some forms. The shallow- and deep-water stromatolites in these reef complexes have certain distinguishing morphological features which may also characterize other ancient stromatolites. The most distinctive of these is the presence of fenestral fabrics in shallow-water forms (also characteristic of Hamelin Pool stromatolites) and their absence in deep-water forms.

Western Australian Proterozoic stromatolites have been shown to have value for inter-regional correlations within Australia. However, some significant anomalies have been found in attempting to correlate with the standard stromatolite sequence in the Proterozoic of the Soviet Union, and there remains considerable doubt as to the extent to which stromatolites can be used for inter-continental correlation.

Introduction

Interest in the study of stromatolites has increased greatly among palaeontologists, sedimentologists, and biologists over the past 20 years, primarily because stromatolites are the principal macrofossils known from the Precambrian, and are potentially useful for biostratigraphic correlation and environmental interpretation.

However, there has been considerable controversy on the validity of correlations and environmental interpretations using stromatolites. Some authorities have maintained that the morphological characteristics of stromatolites are environmentally rather than biologically controlled, and that consequently stromatolite taxa are meaningless in biological terms, and biostratigraphic correlations based on them can have no validity. These workers commonly favour a stromatolite classification based on descriptive geometric formulae. Others believe that evolutionary changes must have occurred in the stromatolite-building algae, thereby resulting in recognizable changes in the stromatolites themselves through geological time. They claim that although environmental factors are often important in controlling the gross external morphology of stromatolites, their internal fabric is largely biologically controlled. These authorities use a binomial nomenclature of "group" and "form" in classifying stromatolites. They

acknowledge that the terms "species" and "genus" should not be applied to stromatolites, as they have commonly been built by assemblages of algae and/or bacteria. Many of these workers believe that stromatolites are of considerable value for inter-regional and perhaps inter-continental correlations in the Precambrian. A recent comprehensive review of the status of world stromatolite research is contained in the volume edited by Walter (1976).

With regard to the environmental interpretation of stromatolites, some researchers have claimed that marine stromatolites are restricted to narrow environmental limits, being virtually confined to the intertidal zone. Others believe that stromatolites have grown through a very wide range of environments, from the supratidal zone to abyssal depths of the oceans.

Research on Western Australian stromatolites has played an important role in the history of debate on these critical aspects of stromatolite studies, and it is to these aspects that I will primarily direct this paper.

The term stromatolite as used in this paper is defined as an organosedimentary structure with vertical relief above the substrate produced by sediment trapping and/or precipitation resulting from the growth of micro-organisms, principally blue-green algae (slightly modified after Awramik 1977).

Historical review

The first description of stromatolites in Western Australia was by Clarke and Teichert (1946) dealing with wrinkled and bulbous structures in algal mats covering the floor of Lake Cowan, a dry salt lake near Norseman. Although Clarke and Teichert did not use the term stromatolite in describing these structures, they would be referred to as such by modern workers.

Fairbridge (1950) was the first to publish a description of ancient stromatolites from this State. He described Proterozoic silicified forms, which he referred to the genus *Collenia*, from what is now known as the Coomberdale Chert, in the area north of Moora. Logan and Chase (1961) subsequently described *Collenia undosa*, *C. columnaris*, and *Cryptozoon frequens* from this formation.

Logan (1961) published a paper dealing with the modern stromatolites of Hamelin Pool, an arm of Shark Bay; this was the first research on Western Australian stromatolites to receive international attention. The Hamelin Pool stromatolites are now recognized as being the best examples of living stromatolites known from modern seas, and the conclusions reached by Logan had a profound impact on stromatolite research for many years. Several subsequent papers have described these remarkable forms, including those by Logan *et al.* (1974), Hoffman (1976), and Playford and Cockbain (1976).

An attempt to use stromatolites for correlation of Proterozoic stromatolite-bearing sequences in Western Australia was published by Edgell (1964). He concluded, contrary to prevailing opinion in Australia at the time, that biostratigraphic correlations could be made using stromatolites, at least on an inter-regional level.

A varied assemblage of stromatolites and a series of large stromatolite bioherms have been described from the Devonian reef complexes of the Canning Basin by Playford and Cockbain (1969) and Playford *et al.* (1976). These are among the best-preserved stromatolites known from middle Palaeozoic rocks in the world. However, their unique importance lies in the fact that it has been possible to demonstrate the original water-depth relationships of the stromatolites, and to formulate criteria for distinguishing deep-water and shallow-water forms.

Modern studies of Proterozoic stromatolites in Western Australia began with the monograph by Walter (1972), in which he described forms from the Hamersley, Bangemall, and Ord Basins in Western Australia, and from other Australian basins. Walter applied methods of stromatolite study developed in Russia, where stromatolites have been studied more intensely than in other countries and have been widely used for inter-regional Precambrian correlations.

The most recent work on Proterozoic stromatolites in Western Australia is by Preiss (1976), describing forms from the Nabberu and Officer Basins. This work is important principally because of the doubt that it casts on the validity of inter-continental correlations in the Proterozoic based on stromatolite groups.

Modern stromatolites at Hamelin Pool

Introduction

Hamelin Pool is a marine barred basin consisting of a broad central area 5 to 10 m deep, surrounded by a sublittoral platform up to 5 km wide, backed by intertidal-supratidal flats. The basin is barred to the north by the Faure Sill, a sand and seagrass bank cut by a number of prominent tidal-exchange channels. The high evaporation and low precipitation in the area, combined with the restricted inflow of normal oceanic water because of the Faure Sill, has caused the waters of Hamelin Pool to become hypersaline, with salinities ranging from 55‰ to 70‰ throughout the year.

Stromatolites were first recognized around the shores of Hamelin Pool by geologists of West Australian Petroleum Pty Ltd in 1954-55, and the first published description of them was by Logan (1961). This paper and the subsequent paper by Logan *et al.* (1964) stimulated interest in the study of stromatolites around the world, and their conclusions greatly influenced the interpretation of ancient stromatolites. As a result it became widely accepted that stromatolites are essentially confined to the intertidal zone, that their morphology is environmentally rather than biologically controlled, and that they have formed solely by the trapping and binding of particulate sediment by algal filaments without any biochemical precipitation. Moreover, because of the supposed lack of biological control on stromatolite morphology, it was generally

believed that biostratigraphic correlations based on stromatolite taxa could have no validity. However, each of these conclusions, founded largely on the early work at Hamelin Pool, has since been disproved or substantially modified.

Distribution

Living stromatolites extend discontinuously around the shores of Hamelin Pool from the intertidal zone to depths of at least 3.5 m on the sublittoral shelf. Logan (1961) had claimed that the Hamelin Pool stromatolites are confined to the intertidal zone, and that as a result the maximum height of individual columns cannot exceed the mean tidal range (about 0.6 m). This conclusion was confirmed by Logan *et al.* (1964) and was extended to embrace stromatolites in the ancient record. However, subsequent work (first reported by Playford 1973) has shown that subtidal stromatolites are widespread at Hamelin Pool.

Logan *et al.* (1974) reported that large subtidal stromatolites occur at a few localities in Hamelin Pool, extending to depths of about 2 m, but concluded that these forms could be "relict" structures which grew originally in the intertidal zone at a time when sea level was lower than it is today. Hoffman (1976), in a summary of this paper, also recorded subtidal stromatolites to depths of 2 m, but he did not imply that they were relics of an earlier low sea level.

Playford and Cockbain (1976) observed that contrary to previous reports, living stromatolites and flat algal mats are widespread over the sublittoral platform fringing Hamelin Pool, and that the stromatolites extend to depths of at least 3.5 m. Furthermore, subsequent observations utilizing low-level colour air photos show that subtidal stromatolites and algal mats at Hamelin Pool are more extensive than the intertidal forms.

In many areas of Hamelin Pool living stromatolites are backed by dead forms in the supratidal zone, and these reach 0.5 to 1 m above mean sea level, commonly forming a series of stepped terraces (Playford and Cockbain 1976). These dead stromatolites are in varying stages of disintegration, and they must have emerged in relatively recent times (perhaps only several hundred years ago). It is uncertain whether this emergence has resulted from tectonic uplift or eustatic falls in sea level, but there is increasing evidence for Holocene tectonism in this part of the Carnarvon Basin, and tectonic emergence of the dead stromatolites is therefore likely.

Morphology and biology

Logan (1961) emphasized environmental controls on stromatolite morphology at Hamelin Pool, but he did not distinguish the various types of stromatolite-building algal mats and the internal fabrics resulting from those mats. It was later shown by Logan *et al.* (1974) and Hoffman (1976) that there are three types of algal mat that build stromatolites at Hamelin Pool: pustular mat in the middle to upper intertidal zone, smooth mat in the lower intertidal zone, and colloform mat in the lower intertidal to subtidal zone. Each of these mats is built by a characteristic association of algae; pustular mat is dominated by *Entophysalis major*, smooth mat by *Schizothrix helva*, and colloform mat by *Microcoleus tennerimus*. These authors also showed that the internal fabrics of stromatolites resulting from the three mat types are different.

These observations on mat distribution and on the relationships between mat types and internal fabrics were generally confirmed by Playford and Cockbain (1976). However, more recent observations show that pustular mat extends from the upper intertidal zone into the shallowest subtidal zone, smooth mat is characteristic of the middle to lower intertidal and shallow subtidal zones (extending deeper than pustular mat), and colloform mat is restricted to subtidal environments, reaching depths of at least 3.5 m. Thus there is a generalized zonation of pustular mat dominating the shallowest environments, followed successively moving into deeper water by smooth mat and colloform mat. Pustular mat results in massive or crudely layered, irregular, coarse fenestral fabrics, smooth mat in laminated fine fenestral fabrics, and colloform mat in weakly laminated, coarse fenestral fabrics.

The most characteristic feature of the Hamelin Pool stromatolites is the occurrence of fenestral fabrics, the largest fenestrae being found in stromatolites formed by pustular mat, and the smallest in those formed by smooth mat. The best-developed lamination is formed by smooth mat, while the poorest results from pustular mat.

Monty (1976) and Golubic (1976) give further details of some aspects of the microstructure and internal fabrics of Hamelin Pool stromatolites and of their biological characteristics.

Logan (1961) concluded that discrete stromatolites occur characteristically around headlands, whereas flat algal mats occur in bays, and this was generally confirmed by Logan *et al.* (1974) and Hoffman (1976). They observed that stromatolites at Hamelin Pool are commonly elongate in the direction of wave translation, approximately normal to the shoreline, and deduced that such elongation in ancient stromatolites is likely to have a similar origin. They also reported that some stromatolites "lean" seaward in the direction of wave translation. Hoffman (1976) noted further that stromatolites in some areas of Hamelin Pool occur in belts parallel to the shorelines, but gave no explanation for this alignment.

Playford and Cockbain (1976) found that although intertidal stromatolites in some areas are concentrated around headlands, in others they are extensively developed in bays. They also found that subtidal stromatolites are widespread in front of both headlands and bays. It now seems that the main requirement for the extensive development of stromatolites at Hamelin Pool is that there be a rocky substrate. This is generally formed of calcrete (over Pleistocene deposits or Cretaceous chalk), or Tertiary Lamont Sandstone, or lithified Pleistocene beach ridges. Where stromatolites have

been localized by beach ridges, they occur in curved bands which are often approximately parallel to the present coastline.

Playford and Cockbain (1976) confirmed that individual stromatolites are generally oriented in the direction of wave movement, perpendicular to the shore. However, they also demonstrated that in some areas rows of stromatolite ridges have grown parallel to the prevailing wind and that the "leaning" intertidal stromatolites lean towards the wind rather than in the direction of wave movement. It appears that the stromatolite ridges (here termed "seif stromatolites") have formed in response to helical water vortices induced in shallow water by strong prevailing southerly winds. These ridges exhibit "tuning fork junctions" opening upwind, and in this respect they resemble subaerial seif dunes (which are thought to have resulted from helical air vortices). However, the mechanism whereby the prevailing wind controls the inclination of "leaning" stromatolites is not fully understood.

Lithification of the Hamelin Pool stromatolites is occurring in both intertidal and subtidal environments, contrary to the suggestion of Logan (1961) that exposure in the intertidal zone is required for the induration of stromatolites. The particulate sediment that has been trapped and bound by algae is being cemented a few millimetres or centimetres below the surface by microcrystalline aragonite. Detailed studies have not yet been carried out on the cementing process to determine whether or not it is wholly or partly biochemical, but it seems likely that algal or bacterial action is at least partly responsible for the aragonite precipitation.

Stromatolites at Hamelin Pool commonly form linear reefs controlled by the existing shoreline or by indurated submerged beach ridges. These reefs are rigid and wave resistant but they lack the skeletal framework required by many reef definitions, having been built by non-skeletal algae. The Hamelin Pool occurrences clearly demonstrate the way in which stromatolites and other cryptalgal bodies, when subject to early cementation, can form rigid wave-resistant bodies, and there is no good reason why these should not be considered as representing a type of organic reef. Many Proterozoic reefs and some Palaeozoic reefs were apparently formed in this way.

Growth rates

Growth-rate studies on intertidal and subtidal stromatolites at Hamelin Pool show that the living forms grow very slowly. The maximum rate of growth observed is less than 1 mm per year, and many forms appear to have virtually reached a state of equilibrium, with growth approximately balanced by erosion (Playford and Cockbain 1976). It is likely that many of the living stromatolites are many hundreds of years old.

Tracks cut through the stromatolites by horse- and camel-drawn wagons (when goods were transported to and from stations around Hamelin Pool by lighter) are still clearly defined at several localities, little or no regrowth of stromatolites having occurred in the tracks since they were last used during the 1930s. This emphasizes the susceptibility of the Hamelin Pool stromatolites to damage by human activities (Department of Environmental Protection 1975, Playford 1976a).

Classification

A geometric system of stromatolite classification, based on the arrangement of crude hemispheroids and spheroids, was proposed by Logan *et al.* (1964), using the Hamelin Pool stromatolites as a principal example. This classification has been widely used, especially among sedimentologists. However, it does not take into account the internal fabric and microstructure of stromatolites, and is regarded as inadequate for detailed studies by many workers (Walter 1972).

Modern stromatolite specialists who have adopted a biostratigraphic approach to stromatolite research commonly use the Russian binomial taxonomy of "group" and "form" in classifying fossil stromatolites. As yet no one has attempted to apply this classification to the Hamelin Pool stromatolites. However, as pointed out by Playford and Cockbain (1976), they could form an excellent basis for testing principles of stromatolite classification, as the diverse living stromatolites have been built by several mat types and extend through a range of environments. If the taxonomic principles applied to fossil stromatolites have any biological validity they should also be applicable to the modern Hamelin Pool stromatolites.

Hamelin Pool stromatolites: is the present the key to the past?

The barred basin forming Hamelin Pool represents an unusual environment in modern seas, and the unique occurrence there of flourishing stromatolites is linked to the hypersalinity of this environment. Hypersalinity has caused a major reduction in the number of metazoan species in Hamelin Pool compared with adjoining less-restricted areas of Shark Bay. A few euryhaline species (such as the bivalve *Fragum erugatum* and various fish) are abundant in Hamelin Pool, but it is clear that algae grazers (especially gastropods) are much reduced. This allows stromatolites and associated algal mats to flourish in Hamelin Pool, whereas elsewhere, in waters of more normal oceanic salinity, they tend to be "nipped in the bud" by metazoan grazers.

The reduction in algae-consuming organisms in Hamelin Pool resembles the situation that prevailed in the world's oceans during the Proterozoic, when few metazoans had developed, allowing stromatolites to develop widely. Stromatolites subsequently declined progressively during the Phanerozoic, as animal life diversified and became more abundant, until today Hamelin Pool is the principal remaining stronghold of marine shallow-water stromatolites in the world.

The history of stromatolite research at Hamelin Pool illustrates the dangers inherent in uncritical acceptance of modern environments as definitive guides to the past, especially when those environments are themselves imperfectly known. Uniformitarian application of the original Hamelin Pool stromatolite model led to the widespread but mistaken belief that ancient stromatolites are strictly intertidal phenomena and their morphology is controlled solely by environmental factors.

Apart from the fact that the original Hamelin Pool observations were inaccurate, there can be no justification for assuming that all ancient stromatolites have formed under conditions resembling those in Hamelin Pool today. The factor of prime importance in development of the Hamelin Pool stromatolites is hypersalinity, and although some ancient stromatolites can be shown to have formed in hypersaline environments, this was not the case for most ancient stromatolites.

This is not to say that the Hamelin Pool stromatolites are of no value in understanding ancient stromatolites. Quite to the contrary, they have much to teach us about stromatolite growth mechanisms and biological and environmental controls on stromatolite morphology. This information is an important aid in interpreting ancient stromatolites, but what needs to be emphasized is that evidence for the reconstruction of ancient environments must be sought primarily in the ancient rocks themselves. Environments that favoured stromatolites in the past do not favour them today; the present is thus only partly a key to the past.

Devonian stromatolites in the Canning Basin

Introduction

Algal stromatolites are important constituents of the Devonian reef complexes of the Canning Basin. These complexes form a barrier-reef belt which extends for about 300 km along the northern margin of the basin, adjoining the Precambrian Kimberley Block. They range from Middle to Late Devonian in age.

Three basic facies are recognized in the complexes: platform, marginal-slope, and basin facies. There are also several named sub-facies, the most important being the reef-margin, reef-flat, back-reef, reefal-slope, and fore-reef sub-facies (Playford 1976b).

The platforms were for the most part built by stromatoporoids, corals, and algae in the Givetian and Frasnian, and by algae in the Famennian. The platform deposits accumulated in near-horizontal beds, commonly with a massive or crudely bedded reef margin. The platforms stood some tens to hundreds of metres above the surrounding inter-reef basins, and were flanked by steeply dipping marginal-slope deposits composed largely of platform-derived debris, with contributions from indigenous organisms and terrigenous sources. Depositional dips in these deposits were commonly up to 35-40° in loose sediments, and up to vertical where algal binding and precipitation occurred together with early lithification. At the foot of the slopes the marginal-slope deposits interfingered with the flat-lying basin deposits, composed largely of terrigenous material.

Stromatolites occur in the reef complexes in the platform and marginal-slope facies (Playford and Cockbain 1969; Playford 1973; Playford *et al.* 1976). In a few areas they extend from the marginal-slope deposits into the adjoining part of the basin facies. Those that occur in the platform facies are believed to have grown in shallow water (less than about 5 m in depth), while the others have grown in relatively deep water (to depths of 100 m or more).

Shallow-water stromatolites

Shallow-water stromatolites and other cryptalgal limestones are widespread in the platform facies of the reef complexes, where they are commonly the principal rock builders, especially in the younger Frasnian and Famennian complexes. Columnar forms occur most frequently in the reef-margin sub-facies, and flat-bedded algal-mat deposits and oncolites are common in the back-reef sub-facies. Fenestral fabrics are characteristic of the shallow-water stromatolites and other cryptalgal deposits of the platform facies, but are absent in the deep-water stromatolites.

The columnar stromatolites of the platform facies closely resemble the modern Hamelin Pool stromatolites in both external morphology and internal fabric. The close similarity between the fenestral fabrics of these Devonian and modern forms is very striking (Playford *et al.* 1976). It is believed likely that such fenestral fabrics are characteristic of shallow-water stromatolites, both modern and ancient.

Deep-water stromatolites

Stromatolites are conspicuous features of some parts of the marginal-slope facies, extending into adjoining parts of the basin facies, and they also occur capping drowned reefs and allochthonous reef blocks.

The marginal-slope stromatolites grew on slopes with original inclinations ranging from a few degrees up to near vertical. Stromatolitic algae are believed to have been responsible for maintaining those depositional slopes that exceeded the angle of rest (35-40°) for loose debris. Both skeletal and non-skeletal algae were involved in the construction of the stromatolites, recognizable forms including *Sphaerocodium*, *Renalcis*, *Girvanella*, and *Frutexites* (although some authorities regard *Renalcis* as a foraminifer rather than an alga).

The deep-water stromatolites are considerably more diverse than the shallow-water forms in the reef complexes. Playford *et al.* (1976) recognized spaced columnar, contiguous columnar, branching columnar, longitudinal, scalloped, reticulate, undulous, and domal deep-water forms. In addition, large stromatolite bioherms up to 1 km across are developed in some areas, overlying drowned stromatoporoid-algal pinnacle reefs. The most impressive of these occur near Elimberrie Spring in the Oscar Range. Similar

82710(2)

stromatolite cappings, but on a much smaller scale, occur on top of allochthonous reef blocks (derived from platform margins) in the marginal-slope facies.

Depth relationships of the deep-water stromatolites have been deduced from palaeobathymetric reconstructions. The depositional and post-depositional components of an observed dip in marginal-slope deposits can be determined using geopetal fabrics (Playford *et al.* 1976), and on this basis palaeobathymetric measurements can be made. Thus, where an observed dip in marginal-slope deposits is solely depositional the difference in water depth between any two points on a bedding plane is the same as the present elevation difference between them. Appropriate corrections are made where post-depositional tilting is involved. This method has been applied at several localities where stromatolites occur in situ in marginal-slope deposits, and reconstructions indicate that some of the deep-water stromatolites must have grown in water as deep as 100 m or more.

Well-developed deep-water stromatolites are associated with strongly condensed sequences (i.e. very slow deposition). They grew on those areas of the marginal slopes that were receiving very little sediment and on bare elevated features such as drowned pinnacle reefs and allochthonous reef blocks. They are best developed in the Frasnian-Famennian Virgin Hills and Napier Formations, especially in the early Famennian parts. Evidence for the condensed nature of the stromatolite-bearing horizons is provided by conodont zones, which are very much thinner than in equivalent sections lacking stromatolites. It is deduced that the stromatolites grew very slowly; the average annual growth rate may commonly have been as low as 2 μm.

Many of the deep-water stromatolites in the Canning Basin reef complexes are coloured bright red, due to the presence in them of finely divided iron oxide (mainly hematite). In some stromatolites there is a pronounced concentration of iron oxide in and around algal filaments, especially those of the genus *Frutexites*, in which the iron content may be as high as 30%. Other algae which commonly show iron concentration are *Girvanella* and (to a lesser extent) *Sphaerocodium*. Microprobe analysis indicates that low concentrations of manganese also occur with the iron-rich filaments. It is believed that bacteria living in association with the algae are most likely to have been responsible for this iron and manganese deposition.

The columnar deep-water stromatolites commonly grew approximately vertically, either towards the light (phototropic) or under the influence of gravity (geotropic). It is not known whether all the stromatolitic organisms were photosynthetic; some stromatolites could have been formed by heterotrophic algae or bacteria.

The deep-water stromatolites grew as hard and rigid bodies; many are encrusted by crinoid and coral holdfasts, and some show evidence of early fracturing, the fractures being filled with early submarine cement or sediment, forming neptunian dykes. Some of the stromatolites have formed primarily through the trapping and binding of clastic particles (including terrigenous detritus) by non-skeletal algae (and/or bacteria) associated with biochemical or inorganic precipitation of cement. Others contain little or no clastic material and such stromatolites were formed primarily or wholly by algal precipitation of carbonate.

Apart from the sessile crinoids and corals mentioned above, the fauna of the condensed sequences associated with the stromatolites is characterized by open-marine pelagic organisms: conodonts, ammonoids, and nautiloids. These fossils are often very abundant, especially in the interareas between stromatolites.

Characteristics of shallow-water and deep-water stromatolites

The characteristics of deep-water stromatolites in the Canning Basin reef complexes are distinctly different from those of the shallow-water forms. These differences are summarized in Table 1. It is suggested that many of these features may be applicable in other parts of the stratigraphic record for distinguishing between shallow- and deep-water stromatolites.

Table 1

Characteristics of deep-water and shallow-water stromatolites in the Canning Basin

Deep-water stromatolites	Shallow-water stromatolites
Fenestral fabrics absent	Fenestral fabrics common
Usually finely laminated	Usually weakly laminated or unlaminated
Diverse assemblage of forms	Columnar forms only, associated with oncolitic and fenestral limestones
In condensed sequences	Not in condensed sequences
Grew on depositional slopes, drowned reefs, and allochthonous blocks	Grew on near-horizontal limestone platforms
Pelagic faunas common	Associated with reefal and biostromal organisms, especially stromatoporoids and *Renalcis*
Some forms encrusted with crinoids and corals	Not encrusted by corals or crinoids
Iron and some manganese precipitation important in certain forms	No significant iron or manganese precipitation
Commonly red or reddish brown	Commonly white or pale yellow

The deep-water stromatolites show some resemblance to ferromanganese deep-water bacterial stromatolites known from modern seas (Monty 1973). Both occur in condensed sequences, are generally finely laminated, lack fenestral fabrics, and are associated with pelagic faunas. Iron and manganese concentrations also occur in both, but these concentrations are much higher in the modern ferromanganese stromatolites.

Proterozoic stromatolites

During the late 1960s the University of Adelaide became the main centre of Precambrian stromatolite research in Australia, under the direction of M. F. Glaessner. He introduced principles of stromatolite classification and methods of stromatolite reconstruction based on serial sectioning that had been applied for some time in the Soviet Union, where stromatolites had been used extensively for Precambrian correlations. Two of his students, M. R. Walter and W. V. Preiss, began a wide-ranging study of Australian Precambrian stromatolites, which is still continuing. Their two principal publications which deal with Western Australian forms are by Walter (1972) and Preiss (1976). K. Grey of the Geological Survey of Western Australia is also conducting research on Precambrian stromatolites from this State.

Walter (1972) described stromatolites from the Early Proterozoic Fortescue Group (ca. 2 400 m.y.) of the Hamersley Basin, the Early Proterozoic Wyloo Group (ca. 1 900 m.y.) of the Ashburton Trough, the Middle Proterozoic Bangemall Group (ca. 1 000 m.y.) of the Bangemall Basin, and the latest Proterozoic or earliest Cambrian Antrim Plateau Volcanics of the Ord Basin.

In addition to these Western Australian occurrences Walter also described Proterozoic stromatolites from the Amadeus, McArthur and Georgina Basins of the Northern Territory and Queensland. His results suggested that stromatolites could be used for inter-regional correlation within Australia, but he noted some anomalies in correlations with the Russian sequence. One of the stromatolite groups *(Patomia)* he recorded in the Early Proterozoic Wyloo Group is indistinguishable from a Late Proterozoic (Vendian) form in the Soviet Union.

Preiss (1976) described an assemblage of Proterozoic stromatolites from the Nabberu and Officer Basins in Western Australia. The Nabberu Basin occurrences are in the Early Proterozoic Earaheedy Group (at least 1 700 m.y.), while those from the Officer Basin are from Woolnough Hills and "Central Neale" (near Yeo Lake) in rocks which may correlate with the Ilma Beds (probable Late Proterozoic).

The stromatolite groups recorded from the Officer Basin are consistent with the expected Late Proterozoic age, based on correlation with other stromatolite occurrences of this age in South Australia. However, the Early Proterozoic Nabberu Basin stromatolites are anomalous, as the stromatolite groups present have only previously been recorded elsewhere from Late Proterozoic rocks—*Minjaria* from the Late Riphean, and *Tungussia* from the Middle Riphean to Vendian of the Soviet Union. *Kulparia*, another form which may be present (recorded as ?cf. *Kulparia*), is known elsewhere in Australia from Late Riphean or Vendian equivalents. It therefore seems that the time range of these stromatolite groups is considerably longer than had previously been believed, assuming that the 1 700 m.y. dating (K/Ar based on glauconite) is correct.

Consequently, Preiss (1976, 1977) advocates caution in dating Precambrian sediments on the basis of stromatolites alone, especially where correlations are made using stromatolite groups rather than forms. Although the Russian biostratigraphic scheme based on stromatolites appears to have validity throughout the Soviet Union, detailed stromatolite studies are still in their infancy in most other countries, and it remains to be seen how much of the Russian biostratigraphy can be applied on an intercontinental scale.

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The contribution of geochronology to Precambrian studies in Western Australia

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Abstract

In 1906, one decade after the discovery of radioactivity, Rutherford demonstrated that the accumulation of radiogenic daughter products in rocks and minerals containing radioactive elements could be used to calculate their ages. This event initiated the discipline of physical geochronology, whose development and application, outlined in this paper, gradually enabled a firm time scale to be established for the study of earth history. Such a scale had a particularly powerful effect on the study of Precambrian rocks, for which no other effective internal age criteria had been available. The U-Pb, Th-Pb, K-Ar, and Rb-Sr methods were successively developed and refined to produce compatible results of great precision; the mass spectrometer played a key part in this process. In Western Australia, an attempt was made to obtain a mineral U-He age as early as 1910, and data obtained at that time were used in 1926 to calculate U-Pb and Th-Pb ages. But the work was not pursued, and geologists were slow to realise the potential of the new discipline; it was not until the early 1960s, some 10 years after the establishment of the first geochronological laboratory in the State, in the Physics Department of the University of Western Australia, that geologists working on the Precambrian came to appreciate the full value of physical age determinations for their work. Since that time, continuing work at the Australian National University in Canberra, and at the Western Australian Institute of Technology, has combined with the more recent work of other groups to produce a good understanding of the broad geochronological framework of the State. Nevertheless, many problems still remain, but newly developing methods show promise for their resolution.

Introduction

With the benefit of hindsight it is clear that the introduction, during the first decade of this century, of rock and mineral age determination by methods based on radioactive decay was an event of crucial significance for geology, in that it initiated the systematic constraint of historical geology within a reliable time scale. However, to contemporary geologists the importance of this event was by no means self-evident, and the development of physical geochronology in relation to 'classical' geology deserves wide attention as an example of the complex processes at work in the progress of scientific ideas.

For Western Australia the subject has special interest, both through the importance of geochronology in a State with such a vast area of exposed Precambrian rocks of different ages, and also because certain important conceptual advances in geochronology were made in Perth. In outlining, in a paper of this length, the progress of geochronology in Western Australia and its impact on Precambrian studies, we have had to assume that the reader has an acquaintance with both the geology and geography of the State. Readers lacking this, but nevertheless interested in detailed studies, will find adequate information in both areas in Memoir No. 2 of the Geological Survey (G.S.W.A. 1975); readers of this paper who wish to extend their knowledge of the development of geochronology will find a book compiled by C. T. Harper (1973) of great interest.

Critical events in geochronology

Discovery of radioactivity

Early attempts to measure geological time were based on such time-dependent phenomena as rates of sedimentation, the rate of cooling of the earth, and the accumulation of sodium in sea water. All these techniques were quantitatively crude, and involved sweeping assumptions, and it was apparent that a new approach to the problem was required. This came about in a curious fashion. In 1896 Henri Becquerel, a French physicist, found that uranium salts placed near a photographic plate in a drawer in his work table had produced an image of a key which was accidently lying on the plate. He realised that the uranium was emitting invisible but penetrating rays—the element was in fact "radioactive".

Rutherford and Soddy, investigating the phenomenon discovered by Becquerel, found that the empirical facts of radioactivity could be explained by assuming that radioactive atoms disintegrated at characteristic rates to form new atoms of other elements. The rate of decay of a radioactive parent to a stable daughter is proportional to the number of parent atoms, N, present. This law of radioactive decay can be expressed as

$$N = N_0 e^{-\lambda t}$$

where N_0 is the number of radioactive parent atoms present at the time of formation of a mineral or rock, t measures the time elapsed since their formation and λ is the decay constant of the radioactive nuclide. It was shown that the decay constant did not vary over extreme variations in the physical environment and has remained unchanged at least over geological time periods.

Chemical methods in geochronology

Lord Rutherford quickly realised that the accumulation of stable radiogenic daughter products, such as helium and lead in uranium bearing minerals, could be used to measure geological time (Rutherford 1906). Unfortunately the only means available at that time to measure helium and lead were chemical techniques, and both these methods had serious shortcomings.

Strutt (1910) showed that helium leaked from uranium-rich ores, even under laboratory conditions, and thus the measured helium ages could only be regarded as minimum estimates. As a result the helium method fell into disuse for nearly 20 years, until Dubey and Holmes (1929) showed that the method could be used to measure the age of common rocks.

After some promising early work on the uranium-lead method by Boltwood (1907) and Holmes (1911), it was realised that radiogenic lead was produced by both uranium and thorium, and since these two elements often occurred together in minerals, it was impossible to disentangle the two decay chains by purely chemical methods. Another problem was the presence of common lead, included in minerals at the time of their formation, which could not be distinguished from the radiogenic lead except by using corrections based on atomic weight determinations. Thus the chemical lead method could only be used for rich uranium-bearing ores and was therefore not applicable to common rocks where the amount of uranium was exceedingly small.

One of the first earth scientists to appreciate the importance of radiometric-based geochronology was Arthur Holmes. He was one of the early proponents of the uranium-lead method, and urged the establishment of a radiometric time scale, and the application of radiometric dating to the crystalline basement rocks of the Precambrian. His book entitled "The Age of the Earth" (Holmes 1927), did much to publicise the emerging field of geochronology, particularly among geologists.

Physical methods in geochronology

A major breakthrough in the extension of geochronology came from a most unexpected direction. F. W. Aston, working almost in isolation at the Cavendish Laboratory, developed a mass spectrograph employing both electric and magnetic fields, which was far more sensitive than earlier versions. By studying the isotopic composition of lead he observed isotopes at masses 206, 207 and 208 (Aston 1927). Aston then analysed a uranium-rich sample of bröggerite and showed that it was highly enriched in lead 206 (Aston 1929). The age reported for this mineral heralded a new era in geochronology, in that this age was based on an isotopic rather than a chemical analysis.

Since that time the mass spectrometer has become the tool of every practising geochronologist—a veritable time machine for the exploration of the past (Harper 1973). Between 1929 and 1941 mass spectrometric techniques developed rapidly, mainly as a result of the work of Alfred Nier at the University of Minnesota. Nier *et al.* (1941) reported the results of isotopic analyses of lead separated from both radioactive and lead ore minerals. The age of one monazite sample gave a $^{207}Pb/^{206}Pb$ age of 2 570 ± 70 m.y., which was the first substantial isotopic evidence of the immense age of the Precambrian. Nier was also instrumental in determining the isotopic composition of uranium (which was a vital factor in atomic energy research), in discovering the geochronologically important isotope ^{40}K, and showing that radiogenic ^{40}Ar could accumulate in potassium-rich minerals (Aldrich and Nier 1948). Nier has rightly been called the "father of modern mass spectrometry".

The emergence of new techniques in geochronology

After a bright beginning early in the present century, geochronology developed slowly. The late 1940s and 1950s however, saw an enormous burst of activity which established the feasibility of the potassium-argon and rubidium-strontium techniques, and extended the traditional U-Pb, Th-Pb method. After World War II isotopically enriched tracers became available, and coupled with further advances in mass spectrometry, enabled very low concentrations of uranium, thorium and lead to be accurately measured. This method of analysis, known as stable isotope dilution, has recently been described by de Laeter and Rosman (1977).

It was now possible to obtain three independent ages from the U, Th-Pb system: $^{206}Pb/^{238}U$, $^{207}Pb/^{235}U$ or $^{207}Pb/^{206}Pb$ and $^{208}Pb/^{232}Th$. Wetherill (1956) used a ratio plot of $^{206}Pb/^{238}U$ against $^{207}Pb/^{235}U$ to show that a phase which has remained a closed system to uranium and lead will have $^{206}Pb/^{238}U$ ages equal to $^{207}Pb/^{235}U$ ages, and that the data for systems of different age will lie along a curved line called "concordia". Phases having the same age, and subject to lead loss or uranium gain will, under prescribed conditions, have data that lie along a straight line which intersects concordia. The lower intersection may represent the time of the

episodic event and the upper intersection the age of the phase itself. The work of Silver and Deutsch (1963) showed that U-Pb zircon analyses could be used to give the time of original crystallization of metamorphosed Precambrian cratonic areas.

The decay of the radioisotope ^{40}K to ^{40}Ar forms the basis of a dating technique which can be applied to rocks and minerals between a few tens of thousand and several billion years old—a broader range than can be determined with other radioactive methods. Because potassium is a common rock-forming mineral and argon is retained in many minerals over geologically long periods of time, most rock types can be successfully analysed by this technique. After the early work by Aldrich and Nier (1948), Reynolds (1956) developed a high-sensitivity mass spectrometer for noble-gas analysis, and a number of studies determined the argon retentivities of a wide variety of geological materials. Application of the K-Ar method to young volcanic rocks has been described by McDougall (1966), whilst the technique has also been used successfully to date the times of reversals of the earth's magnetic field (see for example Cox *et al.* 1968).

However, the K-Ar method had serious shortcomings, most of which were related to the migration of argon in mineral assemblies. Fortunately, a variation of the K-Ar method described by Merrihue and Turner (1966), has enabled the imperfect retention of radiogenic argon, or the presence of excess ^{40}Ar to be measured. This technique is known as the "^{39}Ar method", as it involves the conversion, by irradiation with fast neutrons, of a proportion of the ^{39}K nuclei to ^{39}Ar.

Another new technique that emerged at about the same time was based on the decay of ^{87}Rb to ^{87}Sr (Hahn and Walling 1938). Eleven years were to elapse before Ahrens (1949) published the results of an extensive investigation into Rb-Sr dating based on a spectrochemical rather than a mass spectrometric technique, and showed that it was possible to obtain ages by the Rb-Sr method.

The problem of separating the very small amount of rubidium and strontium encountered in common rock forming minerals in a form pure enough to analyse in a mass spectrometer was overcome by the use of ion-exchange chemistry (Aldrich *et al.* 1953), enabling common strontium to be distinguished from radiogenic ^{87}Sr, and accurate mass spectrometric results to be obtained. Throughout the 1950s Rb-Sr dating was applied to micas and feldspars from a number of rocks, and the method gained increasing recognition. Schreiner (1958) then showed that whole rock samples could be used for Rb-Sr dating in addition to mineral separates.

This observation led to a major advance in Rb-Sr geochronology, in that Compston and Jeffery (1959) were able to show that minerals could lose radiogenic ^{87}Sr some time after crystallisation, but that the radiogenic ^{87}Sr was still retained by the whole rock itself. The Compston-Jeffery model provided an explanation for discordant Rb-Sr ages and showed that primary crystallisation ages could be determined in addition to metamorphic events in isotopically disturbed systems. Further details of this work are given later in this paper. Nicolaysen (1961) used a simplified graphical method by plotting $^{87}Sr/^{86}Sr$ against $^{87}Rb/^{86}Sr$ in which members of a comagmatic suite of igneous rocks which have remained chemically closed to rubidium and strontium form a straight line called an "isochron", the slope of which is related directly to the age of the rocks, while the intercept on the $^{87}Sr/^{86}Sr$ axis defines the value of this ratio in the magma source region at the time of differentiation. The Rb-Sr method has been used more extensively in Western Australia than any other technique.

The impact of modern technology

In the early 1960s geochronology was hampered by poor analytical precision, and the resulting interlaboratory discrepancies made it difficult to compare results on an international basis. As a result of these problems a number of international standards were produced to assist laboratories in producing data of high quality. For example, the Eimer and Amend standard was distributed widely to laboratories involved with Rb-Sr analyses, and more recently the National Bureau of Standards have produced stoichiometric salts of rubidium and strontium of known isotopic composition. Standard silicate rocks have also been used by many laboratories to check their elemental abundance measurements, so that geochronological data can now be compared with greater reliability than in the past.

Commercial mass spectrometers have also improved considerably over the past decade. Technological advances including solid-state electronics, peak switching, on-line data reduction by minicomputers and high-vacuum technology, have greatly improved the precision and speed at which isotopic ratios can be measured, and expanded the range of geological samples that can be used. Improvements in ion-exchange chemistry and the use of low contamination "clean rooms" have also played a major role in improving the quality of the data, and have allowed problems to be successfully tackled which would have been impossible even ten years ago. One of the factors in this technological revolution has been the Apollo programme. Considerable information concerning lunar chronology has been accumulated by a variety of geochronological techniques, in which technical problems of considerable magnitude have had to be overcome. The experience so gained has been of inestimable value to terrestrial geochronology. A further improvement in the comparison and assessment of geochronological data has resulted from new measurements of the decay constants of ^{235}U and ^{238}U (Jaffey *et al.* 1971) and the adoption of a new value of 1.42×10^{-11} yr^{-1} for ^{87}Rb (Steiger and Jager 1977).

Western Australian geochronology

Early ages derived from Simpson's work

The earliest attempt to determine the age of a Western Australian mineral by a method based on radioactive decay was made by E. S. Simpson, then Chemist and Assayer of the Geological Survey of Western Australia, in 1910 (Simpson 1910, 1911, 1912). Simpson had received, in that year, samples of a bright-yellow ochreous uranium mineral, which he named pilbarite, from a pegmatite at Wodgina, in the Pilbara Block. As he was acquainted with the work of Rutherford and Strutt on the use of helium in age determination, he carefully analysed the material for helium, and calculated an age of 13 m.y.; but he pointed out that as it was a secondary weathering product, and in any case may also have lost radiogenic helium, this age probably had no significance.

At about the same time Simpson also fully analysed two associated uranium minerals from the same pegmatite, which he identified as mackintoshite and thorogummite, parental to the pilbarite. An intriguing question then presents itself as to why Simpson failed to calculate the ages of all three minerals from the amount of lead present. He had determined this, and had specifically commented on its derivation by radioactive decay; he was also generally familiar with the work of Boltwood, for he mentions him by name (Simpson 1912), though he does not refer to Boltwood's 1907 paper.

Whatever the reason for this puzzling omission, fifteen years went by before L. A. Cotton, Professor of Geology at the University of Sydney, used Simpson's published analytical results to calculate chemical lead ages for these minerals, and also for fergusonite from another Pilbara pegmatite at Cooglegong, an analysis of which had by then been published by Simpson (1919). Cotton's (1926) calculated ages of 620, 1 475, 1 460 and 3 840 m.y. respectively for fergusonite, mackintoshite, thorogummite, and pilbarite took account of the lead contribution by thorium. Holmes and Lawson (1927) independently revised Cotton's calculations, and the inclusion of the age of "mackintoshite, etc" as 1 260 m.y. in Holmes' (1927) popular book "The age of the Earth", in which it was the oldest age recorded, placed the significance of Simpson's 1910 analytical work before a wide audience.

It now appears that this age is too low by a factor of at least two, and this makes it even more ironic that it was probably largely due to Holmes' book that a widespread belief arose that the Precambrian of Western Australia contained the most ancient rocks of the Earth's crust.

Miscellaneous later results

Simpson did not maintain his interest in mineral age determination, and in a letter of 1927 on Government Chemical Laboratories files he politely rejected a suggestion from Sir Douglas Mawson that he should recommence such work. Chemical lead age determinations were later carried out, in 1953, by the Chemical Laboratories on two samples of allanite, collected by A. F. Wilson from pegmatites in the Fraser Range and at Doubtful Island Bay (Prider 1955). The ages, of 1 210 ± 50 and 1 390 ± 50 m.y., are in good accord with subsequent K-Ar and Rb-Sr work on biotite (Aldrich *et al.* 1959), as well as with more recent Rb-Sr results (Bunting *et al.* 1976).

These isolated results were not part of a continuing programme, and the same comment applies to a group of ages estimated from the isotopic compositions of galena samples supplied by J. D. Campbell and R. T. Prider to J. Tuzo Wilson, of the University of Toronto, in 1953 (Prider 1955). These were the first results for any Western Australian minerals by a method employing mass spectrometry.

Establishment of systematic work in the 1950s

In 1950, on his way to take up an appointment at the Australian National University, Professor (later Sir) Marcus Oliphant visited the Physics Department of the University of Western Australia, and spoke of the need for an Australian research programme in geochronology, particularly in view of the widespread belief that the continent contained the Earth's oldest rocks (Jeffery 1976). Oliphant had worked with Lord Rutherford in Cambridge, and was familiar with the physical techniques used in geochronology.

As a result, two younger staff members, P. M. Jeffery and A. H. Morton, terminated the construction of a small accelerator and began instead to build a mass spectrometer, intended ultimately for a continuing geochronological programme. Jeffery (1976) has given a graphic account of the difficulties involved. The instrument first operated in late 1952, but its performance was not satisfactory, and during 1953 it was decided to abandon the project unless more financial support could be found. Fortunately, a grant became available from the Carnegie Institute of Washington, sufficient not only to bring the home-made instrument into effective operation but also to provide a second, new, Nier-type mass spectrometer. It was on this instrument, commissioned by D. Greenhalgh, that the first isotopic U-Pb age was obtained from a Western Australian mineral. The tanteuxenite used came from a pegmatite at Woodstock, again in the Pilbara Block, and yielded a maximum age of 2 790 ± 25 m.y. (Greenhalgh and Jeffery 1959).

It was only after Jeffery had taken up a Carnegie Fellowship at the Department of Terrestrial Magnetism in Washington in 1955 that the potential of the Rb-Sr and K-Ar methods was fully appreciated, and on his return to Perth programmes in both these methods were begun. Although a number of K-Ar determinations were carried out on micas and feldspars from pegmatites and granites, the main achievements of the group thus established lay in the Rb-Sr method, in which work Jeffery was joined by W. Compston and G. H. Riley.

Towards the end of the 1950s the validity of the Rb-Sr method was being questioned, since

mineral separates from whole rock samples were giving discordant ages. A granite from the Boya quarry near Perth was analysed by Rb-Sr geochronology, together with the biotite and microcline separates. The resultant ages were 650 m.y. for the biotite, 1 290 m.y. for the microcline and 2 430 m.y. for the whole rock (Compston and Jeffery 1959). The authors suggested that the mineral separates had lost a significant proportion of their radiogenic Sr some time after crystallisation, after which metamorphic events caused the Rb-rich minerals to lose radiogenic ^{87}Sr which was simply redistributed within the whole rock system.

The model proposed by Compston and Jeffery represented a most important advance in the interpretation of discordant Rb-Sr ages and established the Rb-Sr technique as a powerful tool in geochronological studies of isotopically disturbed systems (Harper 1973). Fairbairn *et al.* (1961) applied the Compston-Jeffery model to a number of discordant ages from Sudbury in Canada, and concluded that "we therefore regard the whole-rock approach as a milestone in interpretation of discordant Rb-Sr data". The Compston-Jeffery model was elaborated in a number of important publications (Compston *et al.* 1960, Riley and Compston 1962, Riley 1961) which set the seal on this contribution by the laboratory.

An important geological contribution to the programme was made by A. F. Wilson, of the Geology Department of the University of Western Australia. His energetic research interests in the southern Yilgarn Block, and in the Albany-Fraser Province, were a significant control over the material selected for analysis. The seminal 1960 paper by Wilson, Compston, Jeffery and Riley (Wilson *et al.* 1960), in which 36 Rb-Sr ages (19 of them new), 16 K-Ar ages (4 new), and 21 U-Pb ages were presented and discussed together was the first systematic attempt to relate these results to the tectonic evolution of the Western Australian, and in this case also the Australian, Precambrian. Even so, their potential in this respect was restricted, since apart from mineral ages from isolated pegmatites of uncertain geological relationships in the Halls Creek Province, the Pilbara Block, the Northampton Block, and the Albany-Fraser Province, the reported ages were confined to the southern parts of the Yilgarn Block; the main factor in the choice of the pegmatite minerals was, necessarily at that stage, their chemical suitability.

The changed situation of the 1960s

In 1959 it might have been supposed that all was set for a major expansion of geochronological work at the University of Western Australia, but in fact by 1961 such work had ceased (Jeffery 1976). The prime reason for this was probably a growing appreciation, from the practical experience gained, that the establishment and maintenance of a geochronological laboratory of the size and scope that was needed in Australia was, quite simply, an inappropriate task for a comparatively small Physics Department which wished also to retain a range of representative research interests. The decision to terminate such a successful research programme was made easier by a concurrent move by the Australian National University to establish a laboratory better equipped to supply national needs in Canberra, in association with the Commonwealth Bureau of Mineral Resources. Compston moved to that laboratory in 1961, while Riley took up a research fellowship at the Australian Institute of Nuclear Science and Engineering in New South Wales. Coincidentally, Wilson, the major geological contributor in the group, simultaneously moved to Queensland, and "a comprehensive geologic age determination programme which is being developed to outline the geochronology of the Australian continent" (Greenhalgh and Jeffery 1959) was abruptly discontinued.

That Precambrian geochronological studies in Western Australia were not disastrously set back by this event is wholly due to the fact that, from Canberra, Compston retained a strong interest in Western Australian work. This was effectively achieved by initiation of Ph.D. studies in restricted areas, and theses which were completed or initiated in this way during the 1960s include those of Turek (1966), Bofinger (1967), Worden (1970), and Gray (1971). During this period Compston maintained a good liaison with the Geological Survey of Western Australia, and some results were published in association with it (Leggo *et al.* 1965). In respect to Western Australian work, he also joined in geological liaison with other university departments, and encouraged such liaison among his students and colleagues, so that consequent publications result from a wide range of collaborative work.

Two characteristics differentiate the Western Australian work carried out from Canberra in the 1960s from the earlier Perth work. Firstly, the necessity for close integration of field geology and geochronological studies was recognised. The work of Bofinger (1967) on the eastern arm of the Halls Creek Province provides a typical example of this: as a member of the Bureau of Mineral Resources, Bofinger took part in the joint field mapping with the Geological Survey of Western Australia, and collected and observed the geological relations of almost all of the samples he analysed. Secondly, and as a consequence of this recognition, an attempt was made to extend geochronological work more widely over the Western Australian Precambrian. Thus from work during this period results were obtained from the Kimberley region (Bofinger 1967, Bennett and Gellatly 1970), from the Pilbara Block (Arriens 1967, Compston and Arriens 1968), from the Hamersley Basin (Leggo *et al.* 1965), from the Gascoyne Province (Compston and Arriens 1968), from the Bangemall Basin (Compston and Arriens 1968), from the Musgrave Block (Compston and Nesbitt 1967, Gray 1971), from the Albany-Fraser Province (Arriens and Lambert 1969, Turek and Stephenson 1966), from the Yilgarn Block (Turek 1966, Worden 1970) and from 'basement' rocks encountered in petroleum exploration drilling in the Officer Basin (Bofinger 1966), and

the Canning Basin (Johnstone 1961). A noteworthy early publication of this period recorded a pioneer attempt to establish the depositional age of a shale by the Rb-Sr method (Compston and Pidgeon 1962).

Consolidation in the 1970s

It was this emphasis on the integration of field geology and geochronology that brought home to the bulk of geologists concerned with the Western Australian Precambrian in the 1960s that isotope geochronology had become an indispensable tool for the solution of many problems, and a positive demand for results began to grow. Two main factors made it seem unlikely that Compston's laboratory alone could satisfy this. These were, firstly, the constraining effects of the need to define most work in terms of independent higher degree parcels, and an increasing commitment of the laboratory to prepare for and carry out work on returned lunar samples, first received after the USA Apollo 11 mission in 1969.

In response to this situation, we discussed, early in 1968, as representatives of the Physics Department of the Western Australian Institute of Technology (JRdeL) and of the Geological Survey of Western Australia (AFT), the possibility of establishing a co-operative geochronology programme based on mass spectrometric facilities already in operation at the Institute of Technology. The ranges of geological and physical expertise within the respective groups appeared to be potentially complementary, and it was agreed to proceed on a trial basis, with a number of restricted projects.

For these initial projects rock bodies were chosen for which clear-cut geological relationships indicated the likelihood that they would each yield a single age of known significance; and a further restriction was applied that each should be chemically amenable to a whole-rock Rb-Sr isochron approach, using for each sample a combination of X-ray fluorescence analysis of the Rb/Sr ratio and a single unspiked mass spectrometer run for the $^{87}Sr/^{86}Sr$ ratio. One final constraint on project choice should not be overlooked: close liaison was maintained with the Australian National University geochronological laboratory to avoid duplication of work, and this liaison was also crucial in the establishment of experimental procedures.

The anticipated mutual advantages in co-operation between the Geological Survey and the Institute of Technology were amply confirmed in practice. The first results were published in 1970 (de Laeter and Trendall 1970), and a total of 19 papers have appeared from a currently continuing programme. The basic restriction to the Rb-Sr method has been maintained throughout, but no problem which could be theoretically solved by the method is now excluded by analytical constraints, although regard in planning is paid to the desirability of maintaining an acceptable ratio of geologically meaningful results to invested analytical time.

Two important controls over the choice of problem to attack have been the progress of the Geological Survey regional mapping programme, and the conscious attempt to identify priority areas, in which work seems likely to yield the most productive results. Work published so far has been widely distributed over the State, and includes results from the Pilbara Block (de Laeter and Trendall 1970, de Laeter and Blockley 1972, de Laeter *et al.* 1975, Lewis *et al.* 1975, de Laeter *et al.* 1977), from the Hamersley Basin (de Laeter and Trendall 1971, Trendall and de Laeter 1972, de Laeter *et al.* 1975, Hickman and de Laeter 1977), from the Yilgarn Block (Muhling and de Laeter 1971, Bunting *et al.* 1976), from the Paterson Province (Trendall 1974), from the Gascoyne Province (de Laeter 1976), from the Bangemall Basin (Gee *et al.* 1976) and from the Albany-Fraser Province (Bunting *et al.* 1976).

Although we have chosen to regard the re-establishment of geochronological work in Perth as the distinguishing character of the 1970s we emphasize that there was no termination of Canberra work. This continued through the 1970s with the same general policy and objectives that had applied before. However, a significant innovation during this period was the initiation of Pb-Pb work on trace lead in minerals (Oversby 1976), and subsequently of the U-Pb method on extracted zircons. It is a special objective of this work to identify the oldest rocks of the Australian continent. The 3 450 m.y. age for dacite of the Duffer Formation, in the Pilbara Block, recently published by Pidgeon (1978), is the oldest age so far determined from the Archaean of Australia; Pidgeon's continuing work on zircons will be an important addition to Western Australian geochronology. Some work on Western Australian material was initiated and carried out by the Bureau of Mineral Resources in Canberra during the 1970s (Page *et al.* 1976).

In addition to the continuing geochronological programmes in Perth and Canberra, which we have discussed in some detail, the 1970s saw the initiation of some Western Australian work by other laboratories. A mass spectrometry unit established at the Department of Geology of the University of Adelaide in 1972 has published Rb-Sr results from the eastern Yilgarn Block (Cooper *et al.* 1976), and has also worked in the Pilbara Block. Yilgarn Block Rb-Sr results have also come from commercial laboratories in Adelaide (Webb and Watts 1975), some K-Ar work on the Albany-Fraser Province has been carried out at the University of Queensland (Stephenson *et al.* 1977).

The University of Melbourne has a varied programme of geochronological research in Western Australia, concentrating mainly on fission-track techniques, but including ion-probe isotope geochronology; no results have been published at the time of writing. The CSIRO Division of Mineral Physics also has current plans for both Rb-Sr and Sm-Nd studies on Western Australian material.

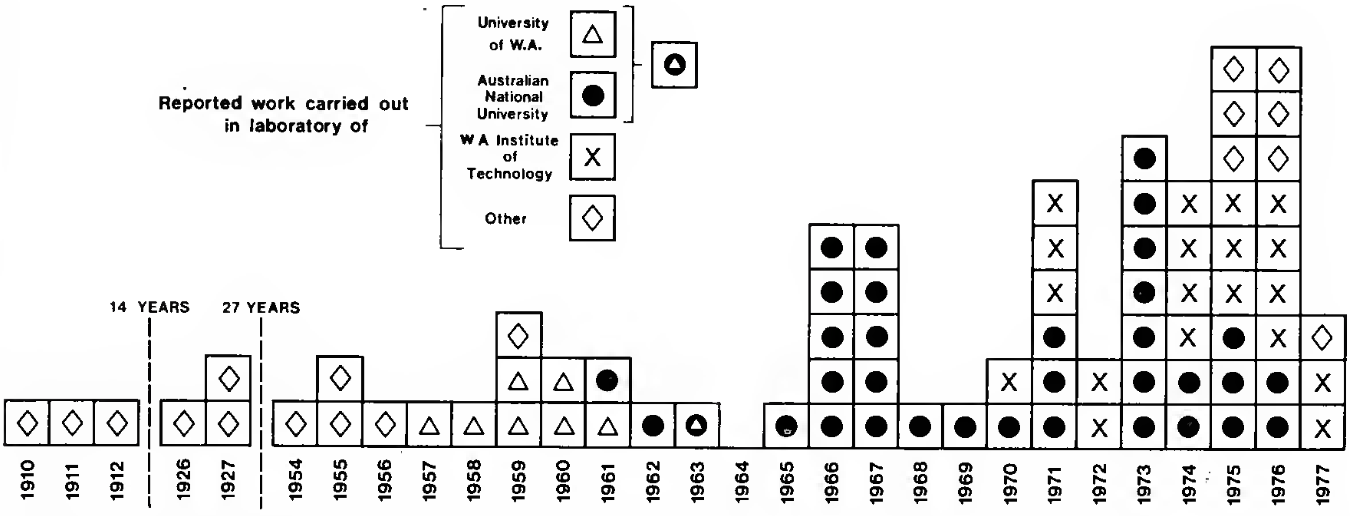

Figure 1.—Chronological summary up to 1977 of all publications including first reports of ages of Western Australian Precambrian rocks and minerals by methods based on radioactive decay. Selected second reports are also included where these augment or upgrade the first.

Thus, at the time of writing, five geochronological laboratories have continuing programmes in Western Australian, while other work is being carried out from time to time. Current planning has the advantage of a reasonably well established time-scale of years for the evolution of the Precambrian rocks.

Publication summary

We have elsewhere presented a complete listing of all first, and some subsequent, publications reporting the results of geochronological work on the Western Australian Precambrian (Trendall and de Laeter 1978). Figure 1 is a graphical summary of the 77 such papers there included. It reflects clearly the phased development of geochronological work described above.

Interaction with geological work

This brief account of the interaction of geochronology with general geological studies must accept, so far as geology is concerned, various review papers as representative of the thinking at the time of their appearance. The situation shortly before the advent of geochronology was well summarised by the then Government Geologist, A. Gibb Maitland (1906). He assigned all "those gneissic, granitoid, and schistose rocks, which" . . . "form the floor upon which the newer strata have been laid down" to the Archaean; his next younger time division was the Cambrian, within which were included, under the name "Nullagine", many of the younger, unaltered, and undeformed sediments, now known to have a wide range of Precambrian ages.

Naive as this view may now seem, a modified form of it persisted until its final concurrent destruction by mapping and geochronology in the 1960s. The modification consisted in accepting a two-fold time division of the Precambrian into an older Archaeozoic (Archaean) and a younger Proterozoic; rocks of the two ages were normally separated by a major unconformity. This modified time classification was used, for example, by Maitland (1919) in a subsequent summary of the geology; in this summary Maitland made no reference to Simpson's (1911, 1912) published attempt to determine the age of uranium-bearing minerals.

In 1930 E. de C. Clarke reviewed the Precambrian geology of the State in a Presidential Address which was published in the following year (Clarke 1931) and illustrates well certain points we wish to emphasize here.

Firstly, Clarke (1931, Table p. 187) essentially accepted the two-fold division of the Precambrian, with a "Great unconformity" dividing various older rocks below from the "Nullagine Series" above. Secondly, the Nullagine Series was correlated between widely separated areas of the State with no Precambrian outcrop continuity—specifically between the Meekatharra, Kimberley, and Warburton areas, and by implication the Nullagine district itself.

Thirdly, although Clarke noted that "there is no certainty in correlating similar rocks of the different districts, many of which are widely separated", he also stated that "Correlation" . . . "can only be made after much fresh petrological detail combined with field observations is available". Like Maitland, he did not refer to Simpson's results, nor did he give any indication either of being aware of Cotton's (1926) or Holmes' (1927) calculated ages from them, or of appreciating the potential value of age determinations based on radioactive decay.

These three points, and among them we emphasize the third, apply to all general reviews of the Precambrian geology of Western Australia published during the 20 years following Clarke's (for example: Forman 1937, Clarke 1938, McKinstry 1945, Prider 1948). Thus Holmes' publication in 1927 of the Wodgina age, on the basis of Simpson's 1910 analyses was met within Western Australia by a total lack of *published* reaction.

The first published reference to the important potential of geochronology for Precambrian correlation in Western Australia was made by Prider (1952), in a summary of the geological structure of the southwestern part of the State. However, two more years passed before Prider (1954) made the *first published reference within Western Australia* to Holmes' (1927) calculation of an age from Simpson's analyses, in a review that summarized all available geochronological information to that date.

In the absence of locally published comment between 1927 and 1952 it is not easy to establish whether Holmes' publication of the Wodgina age was in Western Australia largely overlooked, or whether it was generally known, but not taken very seriously. For information on this point we are indebted to Mr. F. G. Forman. Forman (pers. comm. 1978) is emphatic that Holmes' work was well known to geologists working on the Precambrian at that time, but that there was widely and deeply felt mistrust of the reliability of radiometric age determinations. Prider has pointed out to us that an unpublished handbook to accompany historical geology lectures at the University of Western Australia in 1939 referred to an age of 1 260 million years from a pegmatite in the North-West, although no authority was cited. We accept that the lack of published references to Holmes' (1927) work was not due to lack of either knowledge or interest, but to a doubt shared by most geologists as to its validity. The same feeling is probably echoed for Australia generally by David and Browne (1950), who mentioned the Wodgina age, without citation, and with the unelaborated comment (p. 4) "the results are not regarded as reliable".

After Prider's (1954) first listing of available geochronological results, quickly followed by that of Wilson (1958), the application of geochronological results became common among Precambrian geologists in Western Australia. However, the earlier mistrust in them took some time to diminish, and although individual geologists, notable among them A. F. Wilson, enthusiastically advocated their utility, general acceptance by the majority of geologists working on the Precambrian was finally achieved only when the results were evidently consistent with the time relationships demonstrable from traditional kinds of geological evidence. The best such example is the demonstration by Geological Survey regional mapping during the early 1960s (Halligan and Daniels 1964) that two sedimentary successions, traditionally correlated as "Nullagine", were separated by a major regional unconformity related to intense folding and metamorphism of the older; later geochronology (Compston and Arriens 1968) confirmed this time relationship. Elsewhere within Australia a similar demonstration of the concordance of geological and geochronological evidence was given by McDougall *et al.* (1965).

Comment, discussion, and the future

From the sequence of events we have traced above, a picture emerges for Western Australia of the reluctant acceptance of physical geochronology by a sceptical geological community, as a result of the initiative and enthusiasm of physicists and chemists. Simpson's attempt in 1910 to obtain a U-He age for "pilbarite" was in the vanguard of contemporary international effort, but was not locally appreciated as such. The discovery by Cotton and Holmes, after an interval of more than 15 years, that Simpson's published analyses could be used to calculate chemical lead ages, met a similarly cold response.

We initially found it hard to account for this indifference by geologists, especially during the quarter of a century between 1927 and 1952, to results that, judged on their presently known merits, might be assumed to have been challenging and exciting. For a possible explanation we are indebted to Burchfield (1975), who has traced, in an international context, the bitter dispute concerning the age of the earth that continued through the latter part of the nineteenth century between physics, in the person of Lord Kelvin, and geology. Kelvin, from thermodynamic arguments, proposed a severely restricted age, which geologists, from a variety of uniformitarian considerations, could not accept.

The discovery of radioactivity undermined Kelvin's arguments, and discredited, in the eyes of geologists, the reliability of theoretical physical reasoning as applied to the age of the earth. It was ironic that, within a decade of its discovery, this very phenomenon, that had finally justified half a century of spirited geological opposition, became the basis for physical estimates of the age of the earth which were now unacceptably long, rather than too short. Unhappy to embark on a further half-century of debate, "most geologists simply ignored the new physical results" (Burchfield 1975, p. 179). We accept the apparent indifference of most Western Australian geologists to geochronology as a microcosm of this international situation; it was in essence a negative reaction to the earlier failure of physics, as perceived by geologists, to make a helpful contribution to the problem of the age of the earth.

It is all the more remarkable, in view of this indifference, that the geochronology group established at the Physics Department of the University of Western Australia, was so outstandingly successful, in any terms in which scientific attainment is measurable; its achievements are one of the highlights in the history we have traced in this paper. From discussion with many of those concerned, we conclude that its success cannot be ascribed to any single factor, but that a fortuitous coincidence of many unrelated circumstances combined to produce the final result. Apart from the chance visit of Oliphant, it was fortunate that his suggestion was taken up by a leader, Jeffery, whose infectious enthusiasm was vital to attraet and sustain the interest of able and dedicated students such as Compston, Greenhalgh, and Riley. The prior existence of instrumental skill within the Department was a further prerequisite for success, as was the availability of emergency finance in 1953 when the project was all but abandoned. Finally, it was significant that

Precambrian granitic rocks with an age of about 2 600 m.y. which had been affected by a thermal overprint at about 600 m.y. were available for study. It was the challenge of this situation that produced the Rb-Sr total rock method, which in turn established the laboratory as an international leader in geochronology.

Burchfield (1975, p. 216) has commented that "From the time when Kelvin coupled the first announcement of his results to an attack upon uniformitarianism, until the final acceptance of radioactive dating nearly seventy years later, the question of the earth's age was never entirely free from some degree of tension between physics and geology". Our examination of the Western Australian situation suggests that, although there were earlier exceptions to which reference has been made, the complete reconciliation of geology and physics in this area did not come until the 1960s. The complete fusion of geological and physical skills is now widely accepted, and unreservedly so by us, to be a prerequisite for effective research in geochronology, and it is interesting that this is true both in current practical experience, and in the context of history.

It is inevitable that a historical examination of the kind we have attempted here should lead us to look at the future. There are at least 16 primary natural radioactive nuclides (Rankama 1963), 5 of which have been extensively used in Precambrian geochronology: ^{40}K, ^{87}Rb, ^{232}Th, ^{235}U and ^{238}U. In Western Australia, the ^{87}Rb-^{87}Sr decay system has provided the main basis for establishing the broad time framework which is now known with some confidence. There is much current interest in U-Pb and Th-Pb methods, and the application of these, particularly to zircons and other minerals, is likely to increase. Among the remaining possibilities ^{187}Re and ^{176}Lu have been partially developed as geochronometers (Hirt *et al.* 1963, Von Herr *et al.* 1958), but have not yet been applied to Western Australian samples. The decay of ^{147}Sm to ^{143}Nd is currently emerging as a decay scheme with the special advantage of "seeing through" severe geological disturbance of a sample (McCulloch and Wasserburg 1978), and it is likely that this method will be applied to the Western Australian Precambrian in the near future.

The radioactive clocks, which are the key to our understanding of the chronology of the earth, have progressively yielded their secrets as technological developments have enabled minute quantities of the radioactive elements and their daughter products to be measured with ever greater accuracy and precision. There seems to be no reason to doubt that further refinements are possible as an ever-increasing number of chronometers are available singly or in combination to tackle the problems of Precambrian geology.

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Aspects of Science in Western Australia 1829-1979.
A volume to commemorate the 150th Anniversary of the founding of Western Australia.

History of zoology in Western Australia

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Abstract

Previous histories of zoology in Western Australia are cited (including those of Alexander, Glauert and Whittell) and the survey continued to the present day. Several periods of activity may be reeognised, beginning with the anecdotal records left by the early, mainly Dutch, voyagers, followed by the more substantial ones of the professional naturalists of the English and French marine-exploring expeditions from the late 18th Century onwards. The first colonists in 1829 included many talented observers and collectors, largely amateur, but the next generation settlers were so occupied with subsistence problems that intellectual life ebbed, not to be revived until the late 1880s. Visiting and resident naturalists, and the establishment of the State Museum, resulted in a renewed flowering of zoological activity, often by interested laymen, and supported by private patrons. After World War I these were superseded by an increasing number of academically-trained zoologists, professionally employed and centred on the University of Western Australia and the Western Australian Museum. They added ecology and physiology to the classical-style studies in taxonomy and comparative anatomy and revived field surveys for the documentation of the fauna of the State.

Introduction

A detailed history of the progress of zoological discovery in Western Australia was prepared by W. B. Alexander (1914, 1916, 1916a, 1916b, 1917), the Cambridge zoologist, who was on the staff of the Western Australian Museum between 1912 and 1920. His meticulous studies summarised chronologically all publications dealing with events between 1618 and 1840, with some reference to an apocryphal account dating back to 1499, accepted by some historians but discounted by Alexander.

Major H. M. Whittell and I in our *Birds of Western Australia* (in its five revised editions between 1948 and 1976) expanded Alexander's treatment to modern times but restricting the coverage to ornithological discovery. In addition we divided the chronological account into three fairly well defined periods: (1) the period of the early travellers, 1618 to 1700, when laymen's accounts and anecdotal records predominated, mostly of little scientific merit; (2) the period of the great exploring expeditions, 1791-1826, when discoveries of considerable substance were made; and finally (3) the period of the settlement of the colony, from 1829 onwards. This last period was subdivided into four sections—that dealing with the pioneer observers, 1829 to 1839; that of the visit of John Gilbert and his contemporaries, 1839 to 1843; the so-called "barren years", between 1843 and 1887, and the modern period from 1887 onward.

In 1968 I brought Australian ornithological discovery as a whole into this framework (Serventy 1972) but pointed out that a "barren period" hardly existed as such in south-eastern Australia. Intellectual life in Western Australia ebbed rather low after the comparatively brilliant era of the first colonists. This cultural decline, after the passing of the first generation of settlers—many of them well-educated gentry carrying on the interests of their class in England at the time—has been noted by historians in other disciplines. Thus Kornweibel (1973) in his history of music in Western Australia, refers to the "Doldrums" of the mid-century years and that the revival of musical appreciation did not really come into its own until the 1880's.

Various partial histories of the development of knowledge of the Australian fauna have appeared. One of the most substantial supplements to Alexander's general survey is that by Glauert (1950) on the marsupials of the State. He elaborated on Alexander's treatment, added omitted data and brought the history forward to the mid-1940's. Hedley (1916) summarised the growth of knowledge of the Mollusca of the State from 1801 to 1912. Australia-wide compilations, with marginal relevance to Western Australia, include Gilbert Whitley's summaries of researches (Whitley 1970, 1975). Important historical data are to be found, also, in specialised bibliographies, including that of Musgrave (1932) on Australian entomological writings between 1775 and 1930. Of particular value in this connection is Whittell's *Literature of Australian Birds* (1954) which, besides being an index of published information up to the year 1950, contains an historical account to 1850. Though it is essentially an ornithological history there are references to other animal groups.

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In the present article only scanty references will be made to works already dealt with in Alexander's thorough surveys to 1840, but the few additions to his work, as the result of later discoveries of relevant literature, will be included. As this account is a history, not a complete index to publications on Western Australian zoology, minor or sporadic papers will not be referred to, unless they report something notable.

The period of the early voyages (1618-1728)

The published accounts of natural history observations during this period, mainly by Dutch voyagers between Holland and the East Indies, are more of curiosity value than of scientific worth. Alexander has listed all that are of any relevance to this State.

The ship's company of the *Batavia*, wrecked at the Abrolhos in 1629, were the first Europeans to study an Australian marsupial. The Tammar at the Wallaby Islands was reported on by Francisco Pelsaert. Some problems regarding the ornithology of these islands were resolved when Henrietta Drake-Brockman (1963) deduced that the *Batavia* was not wrecked on Pelsart Island as previously thought but in the Wallaby Group further north. Ornithologists had been puzzled why Pelsaert had not mentioned the enormous flocks of nesting terns and other seabirds on Pelsart Island. Actually he never visited it. Important new information on the zoology of the Southern Group of the Abrolhos Islands was found in the journal of Adriaen van der Graeff, the second mate of the *Zeewyck* which was wrecked on Pelsart Island in 1727. He was the first to indicate that the Wedge-tailed Shearwaters, on which the castaways subsisted, were migratory, first returning to the nesting islands during the third week in August (his actual first date of their arrival being August 20). This detail of the species' life history was not appreciated by modern ornithologists until our own times and it was generally believed that the birds were sedentary (Rogers 1975).

The first European to write on the Rottnest Quokka was Samuel Volckersen, captain of the *Waeckende Boey*, during his search in 1658 for survivors of *De Vergulde Draeck*, wrecked in 1656. The log of his first officer, Abraham Leeman, has been reviewed recently by Tyler and Ross (1977) who interpret the "gulls" on the islet at Sand Knoll Ledge, north of Cervantes, which Leeman's party ate, as fledgling Wedge-tailed Shearwaters.

Alexander (1914) has pointed out that the English translations of the probable meanings of birds names in the old Dutch documents, as given in standard works such as those by Heeres (1890) and Major (1859) "are frequently wrong, as is only natural, since neither of these authors were ornithologists". Alexander sought the advice of a Dutch naturalist, F. E. Blaauw, in correcting them and also gave renderings for the first time, of some Dutch names which Heeres and Major had left untranslated.

The period of the great marine exploring expeditions (1791-1826)

The series of great oceanic expeditions sent out principally by the governments of Great Britain and France began an era of scientific exploration which added notably to the accumulation of zoological knowledge of the Australian region. Captain James Cook and Sir Joseph Banks are the most celebrated individual figures characterising this period but they did not themselves visit the waters of Western Australia. However Banks' journal of his impressions of Batavia (now Jakarta) in Java gives an important contemporary view, scientific and social, of the situation in our near neighbour to the north (Beaglehole 1962).

The earliest of these expeditions to visit Western Australian seas was that in the vessels *Discovery* and *Chatham* in 1791. George Vancouver was in command and the naturalist was the eminent Archibald Menzies. The most productive was undoubtedly the French expedition in the *Naturaliste* and *Geographe*, 1801-1803, under the command of Nicolas Baudin. Alexander (1916) had an unbounded admiration of the ability and dedication of the principal naturalist, Francois Pèron ("as showing the zeal and energy of this great man . . . ") but a rather different picture of Pèron is painted by his commander Baudin in the recently published translation of the latter's log (Cornell 1974). Nevertheless there can remain no doubt of the competence and excellent scientific work of Pèron and his associates.

The work of the several later expeditions surveying Western Australian waters, led by Flinders (1801), King (1818), de Freycinet (1818), Dumont d'Urville (1826) and Wickham and Stokes (1840 in the *Beagle*) has been reviewed by Alexander. All contributed to knowledge of marine and island zoology.

The last of the surveying vessels operating on the western coast was *H.M.S. Herald* (Captain Sir Henry Mangles Denham) which surveyed Shark Bay in 1858. The surgeon, Frederick Matthew Rayner, made important collections of bird specimens here and further north. Chronologically this expedition belongs to a later section in this history. But it may more properly take its place here. Denham is better known for his surveys in New Guinea and eastern Australian waters (Ingleton 1944).

The period of the pioneer settlers (1829-1842)

Both at the Swan River, and earlier at Port Jackson, the first arrivals among the settlers and Government officials exhibited a remarkable zest for natural history inquiry. Many had shared the vogue for natural history prevalent in England since the publication of Gilbert White's *Selborne* in 1789. A new fauna and flora excited latent tastes in such studies. In the east Government officials in the First Fleet were in the forefront in documenting the natural phenomena around them. The first book published about Australia after the settlement, Surgeon-General John White's *Journal of a Voyage to New South Wales* (1789), dealt extensively with the local fauna and flora,

illustrated by many hand-coloured copper engravings. Some of the Establishment officials became more interested in their natural history pursuits than in their official duties. This seemed to be the case with Colonel William Paterson, commander of the New South Corps when Governor Bligh was deposed: he was very greatly attached to botanical studies—and so highly regarded in this field as to be elected an F.R.S.

At the Swan River, as Alexander's literature review indicates, there was a correspondingly keen interest in natural things. Lindley's *A sketch of the vegetation of the Swan River Colony,* published within 10 years of the founding of the settlement, is a graphic illustration of how thoroughly the first settlers had set about botanical studies, largely stimulated, of course, by the presence among them of James Drummond. There is no similar published codification of zoological knowledge but it would be possible to compile one.

There was keen competition among some of the colonists for the natural history spoils available for the inquisitive and acquisitive. Drummond wrote rather petulantly to Sir Joseph Hooker at Kew that a visiting German naturalist, J. A. L. Preiss, who arrived at the Swan River in 1838 and stayed until 1842, was buying up natural history material from the local settlers which Drummond felt should be his prerogative. Preiss was an unusually productive collector: when he left for London he had a collection of 200 000 plants over 600 bird specimens and a big collection of mammals, reptiles, insects and other fauna. He had offered the collection earlier, in October 1838, to the Colonial Government for \$6 000, \$4 000 in "ready money" and the balance in the form of a grant of land, but apparently nothing came of the offer (Glauert 1948). The collections were dispersed over several European museums and were worked over by specialists in ornithology, mollusca and botany, but the whereabouts of much of the material is still unknown (Meise 1951). One interesting specimen probably collected by, or for Preiss, escaped proper scientific study until 1907 when Siebenrock, at the Vienna Museum described what was to become known as the celebrated Short-necked Tortoise, *Pseudemydura umbrina* (Glauert 1955). It had been misidentified by an earlier research worker and the assumption was that it had been part of an original Preiss collection. The species is now confined to two seasonal swamps at Bullsbrook. However, it would appear that at the time of the original Swan River settlement it had a more extensive range. The Sydney botanist Charles Fraser, who accompanied James Stirling in his 1827 reconnaissance of the Swan River, stated when at Upper Swan: "The ridges of the banks are perforated with immense numbers of deep pits, the origin or cause of which we could not at first ascertain. They proved to be made by the natives for the purpose of catching land tortoises, with which these ridges abound" (Hay 1906). This must refer to the Short-necked Tortoise, then aestivating underground in the vicinity of its winter swamps.

The most significant naturalist at the Swan River at this period was John Gilbert, an able collector sent out by John Gould then working on his monumental multi-volume work on the *Birds of Australia.* Gilbert laid the foundations of ornithological knowledge of the south-west of the State. He paid two extended visits: from March 1839 to January 1840 and from July 1842 to September 1843. Few new full species of birds have been found since his time and he was the discoverer of such distinctive new forms as the Noisy Scrub-bird, Western Bristle-bird and Western Whipbird, and provided important data bearing on the contraction of their ranges into the "inner" South-West since European settlement. Gilbert also collected marsupials for Gould. He is probably the only naturalist to have seen alive in its habitat the Broad-faced Potoroo, *Potorous platyops*, and he collected the type specimens of almost half of the species and subspecies of recent marsupials occurring in the south-west. Many of his field notes were used, wholly or in part, by Gould in his *Mammals of Australia,* often without acknowledgement. Gilbert's original notes, in letters to Gould and some notebooks, have been subsequently relocated at odd times and in various repositories and are still turning up (Chisholm 1964). The latest find was in a batch of papers found in the British Museum of Natural History, South Kensington by Ederic Slater of the CSIRO in 1973. His status as a mammal field worker is discussed by Whittell (1954). He joined Leichhardt's expedition in 1844 to Port Essington, to further his collection of natural history material. For his abilities he was promoted in the field to second in command but was killed by Aborigines on June 28, 1845.

Lieut. George Grey, later knighted during a distinguished career, as governor and statesman, in other States, New Zealand and South Africa, explored extensively in Western Australia between 1836 and 1840, collected actively for overseas specialists, and published his observations in two volumes (1841) which are a valuable account of zoological knowledge of the Colony in that period. Observations on the fauna are included in a chapter on the food and hunting of the Aborigines, and there is a catalogue of birds, reptiles and amphibia, with an account of some insects from King George Sound. There were eight plates of reptiles and amphibia and 11 figures of insects. Grey's book is reviewed by Alexander.

A wealth of natural history information is contained in the publications of George Fletcher Moore (1832, 1842, 1884 and various articles in the *Perth Gazette*). Moore was a substantial colonist from Ireland who emigrated in 1830 in the hope of obtaining an official legal appointment as well as becoming a landed proprietor. Before he returned to England in 1852 he had achieved both objectives—he had become the first judge in a civil court, Advocate-General, a member of both the Executive and Legislative Councils, and was acting Colonial Secretary on the death of Peter Broun, as well as being the owner of about 10 000 ha of land in fee simple

and several allotments in towns. His writings reveal him to be an unusually acute field naturalist.

Moore's *Descriptive Vocabulary* (1842) of the local Aborigines is not only a glossary of many terms in use in various places in the South-West, but so annotated as to provide natural history, anthropological and geological information in a succinct way. It is not wholly Moore's work. The manuscript had been placed in his hands "in a very crude state by Governor Hutt, that I should get it published in England." The data in it had been collected by Francis Armstrong, Sir George Grey, Charles Symmons, the Bussell brothers from the Vasse and an anonymous person who "assumed the name Lyon." After he had edited and enlarged the manuscript Moore commented that "I might fairly and truly use the familiar expression, 'Quorum pars magna fui'."

The letter-diaries (published in 1832 and 1884) contain more extended natural history information, which has been reviewed by W. B. Alexander. Information in some missing letters (e.g. in those of the latter half of 1833), and hence unavailable to Alexander, is contained, in part, in the *Perth Gazette* of the period. In the issue of February 1, 1834, in a report by Moore of an excursion which determined the connection of the Avon with the Swan River, there is botanical but no zoological information.

Moore was with Ensign Robert Dale when they collected the first specimen of the Numbat near Mt. Kokeby in September 1831.

The barren years (1843-c.1880)

With the passing of the first generation settlers and the activities of their descendants being almost wholly absorbed with economic survival there was comparatively little leisure or energy left to be devoted to such pursuits as natural history. However, some noteworthy projects were initiated by officers of the Imperial service and other visitors.

In January 1852 William Ayshford Sanford took up appointment as Colonial Secretary and remained until 1855. A Cambridge man, he was interested in ornithology and other zoological studies, becoming after his return to England a well-known palaeontologist, working with Professor Sir William Boyd Dawkins on the British Pleistocene Mammalia. In Perth his most noteworthy achievement, in zoology, was the organization of the Austin surveying expedition to the Murchison in 1854 and working up its natural history results (Austin 1855). This expedition was instrumental in the discovery of the Night Parrot near Mt. Farmer (Serventy 1968). Also Austin's journal shows that they saw the Ghost Bat *Macroderma gigas* at Mt. Kenneth, though this fact was not recognized until years later by Glauert (1950). This would be the first observation of the species in Australia, about a quarter of a century before Dobson formally described it from Queensland.

Another visitor to the State who published on the natural history of the country at this time was Bishop Rosendo Salvado, of New Norcia. His book on Western Australia, with chapters on the flora and fauna, was published in Rome in 1851, five years after he had arrived in Western Australia. Its first English translation did not appear until 1977 (Stormon 1977). The zoological matter in the book is not of very great importance but some interesting direct personal observations are contained in it, intermingled with information garnered from other published accounts, not relevant to Western Australia. There are citations of names and affinities which are not always accurate. Present-day workers are puzzled at the origin of some of the scientific names used by Salvado. Some originate with George Fletcher Moore, 1842—*Anas novaehollandiae* for the Black Duck and *Formica maxima* for the "Lion Ant" or Bullant. But *Pelecanus spectabilis* is a "new" name for the Pelican. It is still unknown how either Moore or Salvado came by these names. Father Stormon suggests that *"spectabilis"* might be a slip for *"conspicillatus"*, the correct specific name for the Pelican.

Among the more valuable personal observations by Salvado is one worth repeating in full: "Not seldom in the winter season, that is, June and July, I have found birds big as a thrush, which had fallen to the ground benumbed by the bitter cold of the night; I would take them up in my hands and not let them go until they had recovered their natural warmth." Salvado has here clearly described a phenomenon, of over-night torpidity, which has only very recently come under the attention of Australian ornithologists (Serventy 1970, Ives 1973). The phenomenon must, however, be of very general occurrence, and will no doubt be the subject of many specialist studies in the future.

This generally bleak period of zoological enterprise was brightened somewhat in 1866 and again in 1868-69, when George Masters was sent by the Australian Museum, Sydney, on collecting trips to the south coast. He obtained several specimens of the now dwindling Noisy Scrub-bird and a large collection of mammals (listed by Glauert 1950).

This period may be said to merge with the next, the Modern Period, with the era of William Webb, of Albany. He worked in isolation from the main communities in Western Australia, but his collecting of animals and plants brought him into contact with eastern states specialists, including Baron von Mueller and W. S. Macleay, who had founded the Macleay Museum in the University of Sydney. Webb also sold natural history material to passengers on overseas ships calling at Albany. The well-known botanical-artist traveller, Marianne North, met him in 1880 and provided the information that Webb had been a convict and was married to an Aboriginal wife. After *The Albany Mail* began publication in 1883 Webb contributed a series of useful natural history articles, the ornithological ones of which are summarised by Whittell, who cited others by title (Whittell 1954).

The modern period (1887 onward)

Introduction

After the English ornithologist Thomas Carter arrived in Western Australia in 1887 there began an era of continuing activity in ornithological studies in the State and there was an accompanying crescendo of general zoological activity. Carter, a pastoralist by calling, was a talented amateur. However, he worked with professional ornithologists both in England and Australia. The important thing was that there was now to be a continuum of contact between ornithologists to the present day.

In addition a number of expeditions, from overseas and within Australia, were mounted to explore the natural history of the inland areas and some islands.

More organized scientific activity became possible when W. B. Alexander joined the scientific staff of the Western Australian Museum in 1912 and the University of Western Australia was founded in 1913, with Professor W. J. Dakin in the chair of biology. Later still, with the re-vitalising of the University Zoology Department by the arrival of Professor H. W. Waring in 1948, the building up of the CSIRO Divisions of Fisheries, Wildlife and Entomology, the appointment of Dr. W. D. L. Ride to the directorship of the Western Australian Museum and the setting up of research staffs in the Fisheries and Fauna (later Wildlife) Department, there was a spectacular upward spurt in the quantity and quality of zoological research. This is continuing with the increase in number of tertiary education institutions.

The Modern Period may be subdivided as follows: (1) the building-up era, to the first World War; (2) under the leadership of the University and Museum, from about 1912 to about 1950; and (3) the present-day era of sophisticated zoological research.

From the arrival of Thomas Carter to the eve of World War I, 1887-1912

Carter did extensive field work in the region of North West Cape, where his sheep station (Point Cloates) was situated (Vines 1968). He laid the foundations of ornithological knowledge of the North-West and early recognized the existence of opportunistic breeding dependent on rainfall. His work overlapped that of another English migrant to the State, who, like him, had had previous experience in modern ornithological practice at home. This was F. B. Lawson Whitlock whose collecting on behalf of various patrons extended knowledge of bird distribution and his material provided the basis for taxonomic work on subspeciation by Gregory Mathews in England. A Victorian ornithologist, A. J. Campbell, visited the southern part of the State in 1889 and a series of reports by him filled in important details of distribution at that time (Campbell 1890).

Two inland expeditions, organized from beyond the State, collected zoological material in the inland areas. The Elder Expedition of 1891 had as naturalist Richard Helms, a remarkably able and versatile German migrant whose collecting in several animal groups was the "chief source of knowledge as to the fauna of the dry interior regions of Western Australia" (Alexander 1916). Helms later worked in Western Australia and between 1896 and 1900 was biologist to the Department of Agriculture. His publications on the East Kimberley and the Abrolhos Islands are particularly important. The other expedition, the Calvert Expedition of 1896 with G. A. Keartland as naturalist, was concerned mainly with ornithology.

Two expeditions from Scandinavia worked in the north of the State. Knut Dahl, a Norwegian, collected in Dampierland in 1895 and added to the knowledge of local birds and mammals (Glauert 1950, Dahl 1926). The Swedish Scientific Expedition of 1910-13, under E. Mjöberg, also worked in the Kimberley Division but as well visited the area between Perth and Albany. Its results were published in 32 parts of the *Svenska Vetenskapsakademiens Handlingar* between 1913 and 1922. The expedition ornithologist, R. Söderberg (1918) was the first to draw attention to a peculiar phenomenon of the arid areas of Australia—the simultaneous occurrence of moult and breeding—an adaptation consequent on irregular opportunistic breeding.

Two considerable British expeditions and one minor one visited the State in the early years of the present century. The era was dominated, to some extent, by Oldfied Thomas, the mammalogist of the British Museum, who was instrumental in setting up the Balston Expedition of the British Museum in 1904-1905 with G. C. Shortridge as collector. He worked in the southern part of the State, on birds and mammals, making substantial contributions to distributional knowledge (Ogilvie-Grant 1909, Shortridge 1909, Glauert 1934, 1950).

In 1912 P. D. Montague, a Cambridge zoologist, visited the Montebello Islands (Montague 1913). The general collections were worked on by specialists and published in the Proceedings of the Zoological Society of London in 1914—Hogg (spiders), Montague (birds, reptiles, fishes and some insects), Rathbun (crustacea), Iredale (molluscs) and Robson (cephalopods). Montague lost his life in World War I.

When Radcliffe-Brown, from Cambridge, visited the State in 1910 on an anthropological expedition, he was accompanied by a young Cambridge graduate, E. L. Grant Watson, as zoologist. Watson collected mainly insects and his account of the enterprise (Watson 1968) would interest present-day expedition members who work under grants or salaries with generous daily field allowances. Watson received no salary and was expected to pay his way by selling specimens he obtained to specialists. He had made arrangements, for example, to receive ten shillings for 20 specimens of beetles, more for any considered rare, and a pound for 12 fleas of any species!

The most productive expedition of this period was the Hamburg South-Western Australian Research Expedition of 1905, under Dr. W. Michaelsen and Dr. R. Hartmeyer. With the exception of the Swedish expedition of Dr. Mjöberg and Montague's Montebello expedition, this was the first fully professional scientific

expedition of this period—in point of time actually the first. The expedition was mainly concerned with invertebrates but collected also reptiles, amphibia and some fishes. The results worked on by teams of specialists appeared in *Die Fauna südwest-Australiens,* in 5 volumes from 1907 onwards (Michaelsen and Hartmeyer 1907-1930). Three reports on the results and abstracts of most of the first three volumes were published locally by Michaelsen (1908, 1911 and 1914). The reports of this expedition provide the first systematic studies of many important invertebrate groups including Annelida, Crustacea, Onychophora and others.

An important generalisation on the relations of the Western Australian fauna to that of the rest of Australia was made by Professor Baldwin Spencer, of the University of Melbourne, after reviewing the results of the Horn Scientific Expedition to Central Australia (Spencer 1896). He introduced the concept of the three faunas—Bassian, Eyrean and Torresian—which has been generally adopted ever since, with modifications (cf. Serventy and Whittell 1976, Serventy 1972, 1973).

From the long-term point of view the most significant happening in this epoch was the establishment of the natural history section of the Perth Museum in 1892 under the curator Bernard H. Woodward. In 1895 its name was changed to the Western Australian Museum (Woodward 1903). Woodward, director of the institution since 1890, energetically encouraged the building-up of its zoological collections even though he himself, primarily a geologist, was mainly concerned with the arts (he was director also of the Art Gallery). In 1894 the Museum engaged the services of a taxidermist O. H. Lipfert, an unassuming but extremely competent naturalist whose role has been generally underestimated. He trained J. T. Tunney as a field collector who between 1895 and 1906 made extensive collections of mainly birds and mammals throughout the State. Lipfert himself also collected widely, his last considerable expedition being with the Canning Stock Route reconditioning party between 1930 and 1931 when he was over 65. But his main occupation at the Museum was the setting up of the displays of mammals, birds and other exhibits in the public galleries. One of the most outstanding was the diorama of the animals near Perth which he set up at the turn of the century, long before such displays became general in overseas museums.

Woodward sought the aid of outside naturalists in running specialist museum activities. The most important was A. W. Milligan, a Perth law clerk, who between 1901 and 1908 held the appointment of Honorary Consulting Ornithologist. He went on numerous expeditions and described the new species of birds that came to the Museum, the most notable of which was the Black Grass-Wren from the Kimberley Division, collected by Dr. F. M. House in 1901 during the F. S. Brockman survey expedition. This bird, though sought for assiduously in the intervening years, was only rediscovered in 1968 by the Harold Hall Expedition of the British Museum (Freeman 1970). Milligan made important, though often faulty, generalisations on bird distribution in the southern parts of the State.

Though he was not a zoologist on the Museum staff at this period mention should be made of the work of Ludwig Glauert between 1909 and 1915 on the cave fossils of the South-West. He captured the popular imagination by showing that such creatures as the Koala, Tasmanian Thylacine and Devil, wombats and other animals thought to be peculiar to south-eastern Australia, had peopled the South-West in Pleistocene and Sub-Recent times. His public lectures on the finds attracted influential audiences, including the Governor of the day. Glauert was transferred from the Geological Survey to the Museum in 1910 and his zoological work will be referred to in the next section.

Another zoological institution came into being in this period—the South Perth Zoological Gardens. The gardens were laid out by the first director, Lieut-Col. E. A. Le Souef in 1897. Le Souef was a member of the renowned zoological gardens family of Melbourne and his brother founded the zoological gardens in Sydney. The history of the South Perth institution and its zoological and acclimatisation activities has been written by Jenkins (1978).

Finally, the Fisheries Department was constituted, following a report on local fisheries administration by Lindsay Thompson, of New South Wales (Thompson 1898). The subsequent reports by the Chief Inspectors (Gale 1900-1911, Aldrich 1912-1933, Fraser 1938-1939), including those of their regional inspectors, Abjornsson and others, provide a wealth of data on the condition of the estuaries and other waters which have been undeservedly overlooked by later research workers. The second Chief Inspector, Fred Aldrich, who held office between 1911 and 1938, was as self-effacing a man as was Lipfert at the Museum, but had conducted useful investigations the results of which are still mostly concealed in departmental files. Chittleborough has recently published one of his pieces of work, on the marine crayfishes (Chittleborough 1967).

In addition to these departmental reports much informative data on fisheries are contained in the minutes of evidence of Parliamentary inquiries into various aspects of fishing, pearling and whaling (e.g. Baglin 1922, Daglish 1906, Holman 1915 and Leslie 1948-1949).

In this period, too, began the first of the State's natural history and biological societies. The earliest was a purely botanical group, the Mueller Botanical Society, founded in 1897, which in 1904 was enlarged in scope to become the Western Australian Natural History Society. In 1909 it was transformed again to become the Natural History and Science Society of Western Australia. All three bodies regularly published their proceedings and papers. In 1913, consequent on events which will be recounted in the next section, the Society became the Royal Society of Western Australia.

The ascendancy of the University and the Museum

Two events in 1912 and 1913 proved turning points in the advancement of zoological studies on modern lines in Western Australia. Bernard Woodward retired from the directorship of the Western Australian Museum in 1914. The post was not filled but the collections were placed in the custody of three Keepers. The Keeper of Zoology was Mr. W. B. Alexander, the Cambridge graduate already mentioned who had joined the museum staff as an assistant in 1912. Alexander vigorously expanded the collections, organized educational displays in the museum on modern lines and by his example stimulated modern ornithological field studies which had a permanent effect on his followers (Serventy 1967).

The other event was the appointment of Professor W. J. Dakin to the first chair of biology in the newly founded University of Western Australia in 1913. Dakin was a marine and freshwater biologist. He enthusiastically threw himself into local researches. In preliminary plankton surveys of the Swan River estuary (Dakin 1916), he established that the phosphorescence in the water was due to a tintinnid ciliate protozoan, that the common jellyfish, *Aurelia aurita,* produced large numbers of ephyrae in June and that it would be possible to work out the complete development of the Swan River prawn from a series of plankton catches—this last anticipation not being realised until recent studies by Fisheries Department biologists. In inland waters he investigated the phyllopods of ephemeral pools and worked on *Peripatus* in damp earth habitats. He organized two scientific expeditions to the Abrolhos Islands during 1913 and 1915, financed by the Percy Sladen Trust. The results were published in a series of papers in the Journal of the Linnean Society of London (Dakin 1916a and 1919, Alexander 1922, Fauvel 1922, Tattersall 1922, Hickson 1922, Clark 1923, Dendy 1924, O'Donoghue 1924). He worked in close co-operation with Alexander of the Museum and the two were involved with the Abrolhos expeditions. Unfortunately both left the State for other spheres in 1920.

It was during their period in Perth that Dakin and Alexander were associated with the evolution of the old Natural History and Science Society into the Royal Society of Western Australia. This happened in 1913. Dakin became the first president and Alexander the second secretary, following a short spell in that office by Mr. M. A. Browne.

After the departure of Dakin and Alexander their posts were filled, respectively, by G. E. Nicholls at the University, and by L. Glauert at the Museum. They did not form the same co-operative team as did Dakin and Alexander, but nevertheless both continued the research tradition laid out by their illustrious predecessors. Nicholls (a London University graduate) who held the biology chair from 1921 to 1947, was essentially a comparative anatomist of the classical school and the graduate research in his department was mainly taxonomic. His own research interests were in the lower crustacea. He was stimulated by Glauert's discovery of a local species of the distinctive freshwater isopod, *Phreatoicus,* and came to specialise on the group, ultimately producing a notable monograph on the phreatoicids from the whole of Australia (Nicholls 1943, 1944). His research students and other associates worked on other crustacean groups. Earlier papers by Sayce (1903), Wolf (1911), who worked on the collections made by the Hamburg Expedition of 1905, and by Dakin (1914) had drawn attention to the rich and varied fauna of phyllopods occurring in the inland claypans and lakes. These were collected and came under study. Milner (1929) worked out a collection of anostracans made by Nicholls himself; K. C. Richardson made a study of conchostracans which remains in manuscript in the Zoology Department; a visiting Swedish specialist on the anostraca, Folke Lindner, was based at the Department in 1936 and 1937 and conducted extended field work which contributed to a substantial part of his massive world revision of the order (Lindner 1941). Nicholls' review (1933) of the fauna of Western Australia is a valuable pointer to the existence of a rich fauna of damp earth and aquatic invertebrates.

Glauert's activities at the Museum between the two world wars were severely hampered by reduced finances, made particularly acute by the Depression. He had to operate virtually single-handed and the widespread collecting which had been a feature of Museum practice before the first World War had to be suspended until revived again later under a new director. Glauert's difficulties during the period and his achievements in spite of them are reviewed in a valedictory article published when he retired from the Museum (Serventy 1957). One minor publication of his, a Museum leaflet proposing popular names for local mammals (Glauert 1928) attained almost instant success in popularising a new name for the Rottnest Island wallaby *Setonyx brachyurus.* This animal had hitherto been referred to as the Short-tailed Wallaby in scientific literature and "Wallaby" by the public. Glauert selected the King George Sound Aboriginal name, Quokka, for it, though the Swan River native name was Ban-gap, or Bunkup as the White settlers varied its pronunciation. "Quokka" became so rapidly accepted, through Glauert's publicity (he was regularly interviewed by the daily press on current zoological news) that most people now consider this name to have been always in use.

This period may be said to mark the withdrawal of the amateur naturalist from his hitherto prominent role as leader in zoological studies in the State and his replacement, naturally enough, by the professional—the trained and better-informed staff and students of the new University, staff members of the Museum and of the scientific branches of State government departments. Later still academic qualifications became an almost essential requirement for entry to the professional ranks.

However, the value of the amateur did not disappear. His role changed. In 1924 an organization ostensibly catering for amateur naturalists was founded in Perth, the Western Australian Naturalists' Club, but it was not until nearly a quarter of a century later that it was able to produce a periodical, the *Western Australian Naturalist,* now in its 14th biennial volume. The Club did not solely remain the prerogative of the amateur, as popularly understood, but proved to be a happy amalgam of the activities of serious amateurs, professionals and interested laymen, continuing the British and European tradition of enrolling persons finding personal pleasure in the study of the natural sciences as well as earning their livelihood in them. The German word, *Liebhaberei,* aptly describes their pursuit. The history of the Club and its achievements has been written by Erickson (1964, 1974). The new role of the amateur in the modern order has been discussed by Serventy (1972, 1973).

Coincidental with these changes of emphasis between amateur and professional in the development of zoology in the State, which were subtle and gradual, was the disappearance of the private patron, or gentleman collector. In the absence of appropriate institutions these people had virtually subsidised natural history in the old days, not only by sending out collectors at their own expense as did John Gould in England and W. S. Macleay and H. L. White in New South Wales, but paid visiting and resident collectors for specimens. Both patron and field collector were dedicated to advancing natural history knowledge and commercial profit was a very low priority, if considered at all. The example given previously of how a keen young Cambridge graduate, E. L. Grant Watson, was able to come to Australia in 1910 for a pittance was not unique. That class of enthusiast has by no means disappeared, but changing opinions on collecting and the attitude of many Museums have contributed to a situation where natural history studies involving field collecting have become virtually a "closed shop" to institutions and their members.

Parallel with these changes and no doubt related to them in a subtle way, is the altered attitude of the public to Zoology in this State. Mr. Jenkins in his presidential address to this Society in 1965 (Jenkins 1965) drew attention to the fact that membership of the Royal Society remained virtually static between 1923 and 1965. However in earlier years the "influence they wielded was disproportionately large." He attributes this to the fact that in early years the membership ranks included most of the influential people of Perth—the leading statesmen, members of the judiciary, leading clergy and merchants and socially prominent citizens. In recent times membership is "attracting mainly working scientists." The annual general meetings and conversaziones used to be important events in Perth's social calendar and the Society's ordinary meetings were reported regularly and fully in the morning newspaper. A presidential address by Bishop (later Archbishop) Riley in 1907 was published in full and other meetings might receive up to two columns of newspaper space. Other scientific news received similar treatment. Lectures at the Museum by Glauert in 1914 on the cave fossils of the South-West drew large audiences, which included the Governor, Sir Gerald Strickland, with extensive press coverage. Another lecture by Glauert to the Western Australian Naturalists' Club in 1925, introducing to the Perth public the concept of continental drift as an explanation of fauna distribution, occupied a full column. Interviews with Perth zoologists, such at Glauert and Lieut.-Col. E. A. Le Souef, of the South Perth Zoo, on contemporary zoological news were commonplace. In recent years such reports became brief and occasional, and usually restricted to bizarre happenings of the "man bites dog" category. But latterly the publicity tide shows signs of turning. Specialist reporters on the *West Australian* like Catherine Martin (medical biology), Alex Harris (general science) and Michael Zekulich (agricultural science) cover the local scientific scene intelligently and in depth.

The modern sophisticated period of research

As with the beginning of the previous epoch the present one, now in progress, coincided approximately with the appointment of new heads to the Zoology Department of the University of Western Australia (in Professor H. W. Waring) and of the Western Australian Museum (in Dr. W. D. L. Ride). The rejuvenation of research and exploratory activity in both institutions, made possible also by an increase in funding and in staff numbers, has been dramatic. This new epoch was also notable for the increased extension into this State of the research activities of the CSIRO (in fisheries and oceanography, wildlife and entomology) and the expansion of the research programmes within the State Departments of Agriculture and Fisheries and Wildlife. The progress in research activity was accelerated when additional tertiary educational institutions were formed—the Western Australian Institute of Technology and Murdoch University.

Professor Waring (Liverpool University), who joined the University Zoology Department in 1948, introduced physiological and ecological teaching and research into the University and stimulated an active group concerned with marsupial eco-physiology. This was centred on a biological research station established in 1954 at Rottnest Island with the Quokka as the main study animal. The project was extended to a field station at Jandakot. Waring's work was widened by A. R. Main's studies on the biology of frogs. Research students from this training centre now occupy important chairs and other senior posts throughout Australia as well as abroad.

Ride, fresh from a vigorous research school at Oxford on vertebrate biology, expanded the scope of the Museum. He demonstrated the truth of the principle, which Glauert had been unable or unwilling to grasp, that "people are able to create funds", if a worthwhile case can be made out to government treasuries or private

patrons. A large increase in funds became available to the Western Australian Museum which enabled the scientific staff to be vastly enlarged allowing an active resumption of the exploration work which had characterised the Museum between 1895 and 1906.

The Fisheries and Fauna (now Wildlife) Department became similarly rejuvenated under another like-minded individual. This was A. J. Fraser who came from the New South Wales Fisheries Department to be Chief Inspector at Perth in 1938—his title was later changed to Director. He was an administrative officer and not a biologist, but he had a remarkable insight into how such a department should develop as an effective instrument into the research and control of exploited natural resources. He created the department as it now is, with a trained research staff. In the early stages of the process he enrolled outside scientists in a committee to plan research enterprise, a body which has now become the W.A. Wildlife Authority within the Department. Working in concert with the Museum the Department has begun a systematic zoological survey of key faunal areas throughout the State. Publication of results are made by both institutions on a scale never attempted in the past.

The relevant activity in the zoological field, within the Department of Agriculture, concerns investigations on species considered harmful to the farming and pastoral industries. The work is based on a modern laboratory complex at Forrestfield.

The major achievement of the CSIRO in terrestrial zoology was the establishment of the Wildlife Research Station at Helena Valley in 1966, and of which the present head is Dr. Stephen Davies. The work organized there is mainly ecological and ethological.

In marine zoology the CSIRO Division of Fisheries and Oceanography has conducted local research since 1943. Prior to that period some marine surveys had been made by the Commonwealth Government in the research trawler *Endeavour*, under H. C. Dannevig (Dannevig 1913). His studies in the Great Australian Bight extended into Western Australian waters. The biological results, including taxonomic studies on many groups, were published in six volumes of reports between 1911 and 1933 by the Commonwealth Department of Trade and Customs. The CSIRO surveys in the Fisheries Research Vessel *Warreen* (Captain C. E. Pedersen) from 1947-1949 were extended later in vessels of the Royal Australian Navy on hydrographic and plankton investigations. The Division operates in active cooperation with the State Fisheries and Wildlife Department.

The new modes of transport now available to the field worker on land, operating as a member of a well-planned team of several specialists, contrast markedly with the facilities available to their predecessors. Whitlock in 1909 travelled to Wiluna by a camel team; Carter, 30 years after he first arrived in the North-West, describes his first motor car trip in 1916. Four wheel drive vehicles and aircraft make the most inaccessible portions of the State available to zoological survey teams and the impressive modern publications of the Museum and Department of Fisheries and Wildlife are now documenting the fauna of the furthest ends of the State.

But, curiously, the South-West corner in spite of 150 years of settlement, still provides zoological spoils of intense theoretical significance. In 1971 A. R. Main discovered *Peripatus* on the Swan Coastal Plain south of Perth (Van der Lande 1978) after it was universally believed that this creature occurred only in the Darling Range plateau. Rosen (1974) demonstrated his belief in a lengthy and elaborate paper that a diminutive fish found in a small brook near Shannon River in 1959, and named by Mees (1961) *Lepidogalaxias salamandroides*, was not a primitive galaxiid but a member of a Northern Hemisphere grouping, the esocoids, or pikes, hitherto unknown from any southern continent and presenting baffling questions as to origins. Rosen's suggested affinities have been treated with some reserve by other zoologists. However, whatever its relationships *Lepidogalaxias* must be regarded as an extraordinarily interesting survival of an ancient fauna. It occurs now in the extreme south-west corner of the State which is remarkable for the number of animal species of very circumscribed ranges—in freshwater fishes (Mees 1961), frogs (Main 1965), and freshwater crustacea of the jilgie-koonac assemblages (Riek 1967). Its present dependable climate emphasises the point made by Gentilli (1949) that throughout the period of climatic changes during the Pleistocene this has been a humid refuge. It deserves a thorough zoological survey and in groups other than birds and mammals which have been the preoccupation of many faunal surveys of the past. *Lepidogalaxias* was first picked up by casual nonprofessional collecting in 1959; it could so easily have remained undetected to the present day. No large area in this South-West corner should be subject to any extensive habitat despoliation—for developmental purposes—until adequate biological surveys have been made. The miscellany of information provided by Nicholls (1933) on the extent of a damp earth and freshwater fauna in the South-West, still largely unworked, lends particular cogency to his plea at the time for "an immediate and coordinated investigation" into it.

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The Western Rock Lobster, *Panulirus cygnus*

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Abstract

The supervision of the rock lobster industry and the management controls that have been introduced have been constantly reviewed so that Western Australia's multi-million dollar industry stands today as one of the few fisheries that can be said to be properly managed. The management strategy has been determined by co-operative decisions between State and Commonwealth fisheries institutions and it has been based on reliable catch and effort data collected since the post-1945 expansion of the fishery, a broad understanding of the species biology after much research work by many scientists, and the application of modern fisheries models to assess levels of fishing effort and the possible effect on the stocks.

Introduction

The western rock lobster forms the basis of a multi-million dollar industry which began as an incidental fishery in the early 1900s when pots were pulled by hand from sail-powered fishing boats and the rock lobsters were mostly sold direct to the housewife by the fishermen.

Little management of the fishery was needed in those times even though, as early as 1897, a regulation was introduced to prohibit the sale of any rock lobster less than the legal size; the regulation, announced in March 1897 set a minimum legal weight of 8 oz. whieh was altered in September of the same year to 12 oz.

The control and management of the fishery has been the responsibility of the State Department of Fisheries and Wildlife and the Departments' management policy has always been based on the best research information available. Early research on the fundamental biology of this species was commenced in the 1940s by the CSIRO Fisheries Division through the efforts of the late Dr. K. Sheard (Sheard 1962). Due to the expansion of the State Fisheries Department's research and management unit and the recent major effort on larvae by CSIRO Fisheries and Oceanography Division, 6 scientists are currently engaged in research on the western rock lobster. At the conclusion of this present review a full list of the publications relating to research on the western rock lobster is presented.

The species (*Panulirus cygnus* George 1962) is endemic to Western Australia, occurring along the continental shelf of the west coast from North West Cape (21° 45′S) to Cape Leeuwin (34° 22′S). Fishermen expanded their operations from the two early centres at Fremantle and Geraldton and they now set their pots over an extensive area from the shallow coastal reefs to the edge of the shelf at 200 m. The present flourishing fishing centres are scattered along the west coast shelf at Kalbarri, Abrolhos Islands, Geraldton, Dongara, Cliff Head, Jurien Bay, Leeman, Cervantes, Lancelin, Fremantle and Bunbury. The annual production is approximately 8 000 tonnes, 95% of which is exported to the U.S.A. market as frozen uncooked tails.

In the mid 1960s, a serious concern was expressed by the scientists and the fishermen because the catches resulting from the rapid expansion of boats, men and pots in the previous 5 years or so had not resulted in a proportionate return to the fishermen. Thanks to the foresight of early fisheries administrators, records of catch and fishing effort had been gathered and as a result of intensified research on these records and a better understanding of the biology of the rock lobster, rigorous limitations were able to be placed on the total fishing effort to halt the decline in catch per unit effort. This was successfully achieved by limiting the number of pots permitted by each boat and restricting the total number of boats in the industry.

Annual production was maintained at a reasonable level but more recent research has shown that effort was again increasing due to an increase in the number of pot lifts over the season since fishermen were working more efficiently and more frequently than they had in the past. So in 1978 the length of the season was reduced by 6 weeks to assist fishermen to maintain a viable economic return.

Constant research into the best management techniques has proved that a natural fishery resource *is* capable of adequate management and the Western Australian rock lobster industry stands today as one of the very few fisheries in the world that can be regarded as well managed.

Because of this research and the results produced by the Western Australian scientists studying the western rock lobster, Perth was chosen in 1977 as the venue for a week-long Australian-American "Workshop on lobster and rock lobster ecology and physiology", the proceedings of which have been recently published (Phillips and Cobb 1977).

General biology and environment

In addition to the commercially important western rock lobster, there are 6 other species of rock lobster in Western Australia only one of which is commercially important. This is the southern rock lobster, *Jasus novaehollandiae* that is fished in south-east Australia. In Western Australia however, its density is not sufficient to support more than small catches at Esperance and Albany. Along the northern coast, 5 species of very wide ranging tropical rock lobsters (*Panulirus* spp.) are found in moderate concentrations in shallow reef and coral outcrops. These species have separate environmental preferences, are restricted in depth to the shallow reefs and do not support continuing catches (George 1968, 1974).

The western rock lobster occupies a subtropic (intermediate) geographical position between these southern and northern zones and occupies much of the relatively wide continental shelf that extends seaward from the west coast. The continental shelf has been subjected to significant sea level changes in the past and the former coastal fringing limestone reef flats now form lengthy submarine "ledges" that provide shelter for the rock lobster. It is a gregarious species and dense groups of several hundred can be found packed closely together in the undercut ledges of these submarine features.

The south-west swell that strikes the west coast is a major physical factor that results in both the constant wave action on the shallow reefs and the deep surges that are a fairly consistent feature of the submarine ledges. The seaweed kelps provide mobile cover around and over the entrances to the undercut ledges. The fauna and flora associated with seagrass beds and reef flats (molluscs, worms, coralline algae, seagrass itself and small crustacea) provide most of the food supply for the rock lobsters. (Joll, pers. comm.). Their feeding forays are usually restricted to hours of darkness; bright moonlight nights drastically reduce the catch in pots and most fishermen reduce their fishing effort during these periods. Predators on the rock lobsters include octopus (Joll 1977) as well as large predatory fish including sharks.

The western rock lobster is regarded as a "slow grower". Chittleborough (1974d) maintained and grew juveniles in the laboratory, indicating a growth-to-maturity period of about 6 years and achieved successful mating and egg carriage under these conditions. Growth occurs only after a moult when the old hard exoskeleton is shed and a new soft one is expanded to its new size by absorption of salt water. Food requirements and the general physiology of the rock lobster alter dramatically before, during and after each moult (Dall 1974a, b, 1975a, b, c, 1977; Dall and Barclay 1977) and they remain deep in their shelters until the new shell hardens in about 7 days.

At the time of adolescence, most if not all, individuals go through a distinct phase known as the "white" phase. The characteristic red-brown colour of the species is not present in the newly moulted shell which is parchment to light pink in colour; red pigment is gradually added to the shell until, after about 3 weeks, they are indistinguishable from the normal coloration. The white phase occurs regularly in November-December of each year in the shallower waters and a rapid offshore migration occurs during the "white" fishing season (George 1958b).

The sexes are separate in *P. cygnus* and sex ratios in the adult stock approximate 1:1 but because of differences in availability this ratio may vary significantly in pot catches (Morgan and Barker 1974). The size at first maturity of females and the mean size of breeding females varies significantly throughout the range of *P. cygnus* with the size at first maturity ranging from around 80 mm carapace length in the northern areas of the fishery to around 95 mm in southern areas (Morgan and Barker 1974). No information is available on the size of first maturity of males although it is probably similar to that of females in the same area.

Mating takes place in July-August and the female carries the black sperm packet (known locally as a "tar-spot") until November-December when the eggs are extruded and attach themselves to the pleopods. Fecundity varies linearly with the size of the rock lobster, a 100 mm carapace length female carrying 460 000 eggs (Morgan 1972). The eggs are carried on the pleopods for up to 6 weeks, depending on the water temperature, before hatching into the first phyllosoma larvae that peak during December and January.

Larvae and juveniles

Studies of the rock lobster larvae have been directed mainly towards understanding their movements in space and time and their ecology. Complementary investigations have also been made to measure the numbers of larvae that return to the coast at the end of the planktonic phase of the life cycle.

The newly hatched larvae or phyllosoma, rise up from the bottom, concentrate at the surface and become part of the plankton. The body of the phyllosoma is flat and leaflike with long legs and protuberent eyes. As there is no pigment or calcium in the skeleton, the body is colourless and transparent. The phyllosoma larvae swim actively toward a weak light source (Ritz 1972b) by beating their "feathery" legs and most movements are directed to rising in the water column since cessation of beating results in a slow descent. The phyllosoma larvae undergo a daily vertical migration in the upper part of the water column, rising towards the surface of the water toward dusk and then descending to lower depths as dawn approaches (Ritz 1972a). In their early stages they are

transported offshore into the Indian Ocean by the effects of wind-driven surface transport acting on the larvae while they are at the surface at night (Chittleborough and Thomas 1969).

The larvae remain in the phyllosoma stages for 9 to 11 months during which time at least 9 phyllosoma stages are recognisable although the number of actual moults is considerably higher than this (George and Cawthorn 1962, Chittleborough and Thomas 1969, Braine *et al.* in press). The first phyllosoma stage is less than 2 mm in length and because they are almost transparent, are only just visible to the human eye; by the last phyllosoma stage, they are about 35 mm long.

The full extent of the larval distribution is not known but significant numbers of larvae have been caught during the intensive CSIRO Fisheries larval research programme as far offshore as 1 500 km (Phillips *et al.* in press). Less is known about the actual return paths of the larvae to the coast of Western Australia. Although many larvae are lost during the long period in the plankton, the survivors are eventually transported back to the edge of the continental shelf of Western Australia by the ocean circulation (Phillips 1977), the greater number arriving between August and December each year.

From this point the larval cycle is completed by the transparent puerulus stage which is similar in shape to the adult. The puerulus stage metamorphoses from the last phyllosoma stage just on or just beyond the continental shelf and then actively swims across the shelf and settles in the shallow reef areas along the coast (Phillips *et al.* 1978). Collecting devices made of artificial seaweed (Phillips 1972) have been designed specially to catch the settling puerulus and by their use, the times and relative densities of settlement from year to year have been able to be compared (Chittleborough and Phillips 1975, 1977). Settlement follows a lunar periodicity with catches being largely confined to the new moon period (Phillips 1975).

The settling puerulus moults into a small pigmented rock lobster about 3 cm long, similar to the adult. These juvenile rock lobsters remain in the shallow coastal reefs (depths of 1-20 m) for 3 to 6 years before migrating out into deeper areas on the continental shelf (Chittleborough 1974d).

Population biology

Much of the research effort which has been expended on the western rock lobster has been on those aspects of its population biology which are of direct importance in making decisions which affect the management of the fishery. Apart from the routine collection of catch and fishing-effort data for use in surplus-yield models these data have included (a) estimates of growth and mortality rates for use in various dynamic pool models of the fishery, (b) information on reproductive dynamics for assessing the likely impact of fishing on the reproductive potential of the stock and (c) various other biological data which have been used to answer more specific regional problems.

The "whites"

P. cygnus is unique among the world's commercially fished rock lobster stocks in that a significant part of the commercial fishery is based on pale coloured, newly moulted migratory animals locally known as "whites". Studies by George (1958b) established that these "whites" are all immature animals and move offshore from the shallow water reefs (where they have spent their early juvenile life) to deeper waters. This late November migration may take the animals on a journey of 25 km or more to an area which presumably is better suited than the inshore areas for the later release of the planktonic larvae. Since the "whites" are newly moulted animals their food requirements are high (Chittleborough 1975) and consequently their catchability by baited pots is likewise high (Morgan 1974b). This results in high catch rates being aehieved by the commercial fishermen in late November and December and it is during this 6 week period that about one third of the annual catch is taken.

Growth

Since, like all other crustacea, *P. cygnus* grows by moulting, the growth process may be considered to be a combination of two factors—the moult increment (the size increase at each moult) and the intermoult period (the time between moults). Field-tagging studies invariably are difficult to interpret in this light since the observed growth between release and recapture will consist of the unmeasured contributions from these two growth processes. Studies in aquaria however have been more fruitful and have enabled meaningful interpretation of field-growth studies.

The intermoult period increases with size in *P. cygnus* and for animals held in aquaria at 25°C the intermoult period is about 100 days for an animal of 76 mm carapace length (Chittleborough 1974d). Chittleborough (1976a) and Morgan (1977a) have shown that moult increment increases with age until the second year of post-larval life, then remains constant during the third year and then decreases with increasing age. The combination of these two processes results in a grown-in-length curve which approximates the von Bertalanffy (1938) curve and this curve has been used in the biological models of the fishery (Morgan 1977a).

Although the "average" growth curve has been used in biological models, growth rates in the natural population exhibit large variations as a result of the influences of limited food resources, high densities of rock lobsters (Chittleborough 1976b) and temperature variations (Morgan 1977a). In addition, animals held in aquaria were shown to exhibit a smaller moult increment with a mild deficiency of oxygen while frequency of moulting was reduced when animals were held in isolation (Chittleborough 1975).

Mortality

Mortality rates in *P. cygnus* may be considered in two parts, those produced by fishing operations (the fishing mortality rate, F) and those produced by natural causes such as predation (the natural mortality rate, M). Since, like all other crustaceans, *P. cygnus* cannot be individually aged, the usual methods of fisheries population dynamics of comparing the abundance of age classes to calculate F and M cannot be used and so alternative methods have been necessary. These have included direct estimation of M from tagging studies (Chittleborough 1970, Morgan 1974a) and the use of length/frequency data to estimate F and M (Morgan 1977a). These methods have indicated an annual value of M of about 0.2 (equivalent to 18% mortality each year) and a value of F of about 1.0 (equivalent to 63% mortality each year) for recent years. Thus, mortality due to fishing comprises some 80% of the total mortality suffered by legal-size rock lobsters.

Management of the fishery

Since the start of the commercial fishery in 1944/45, both the catch and the amount of fishing effort expended to take that catch have increased dramatically (Table 1). This has resulted in an inevitable decline in the catch per unit of effort. During the 1940s and 1950s management of the fishery was by means of a legal minimum length only, since the amount of fishing effort was relatively small and the catch per unit of effort was high enough for those engaged in the industry to achieve a satisfactory return from their fishing activities. In 1961, the Western Fisheries Research Committee met under the chairmanship of the then Director of Fisheries to co-ordinate the research efforts of State and Commonwealth programmes to assist in management not only of rock lobsters but of all the State's fishery resources.

As fishing effort further increased and catch per unit of effort further decreased it became apparent from the analyses of the available catch and effort data that more stringent management measures would be necessary to achieve the dual aims of providing a near maximum total catch and of providing a reasonable return (in terms of catch per unit of effort) to the individual operators in the fishery. The most direct way in which this could be achieved was by a limitation of effort policy and it was this strategy which was adopted by the State Government in 1962. The methods used to limit fishing effort at that time were a restriction on the number of vessels entitled to fish for rock lobsters and a limit on the number of pots each vessel was entitled to use. This pot allocation was based on boat length and was fixed at 3 pots per foot of boat length with a maximum of 200 pots per boat.

Later, a boat replacement policy was introduced which restricted a replacement vessel to the same size as that vessel which was being replaced. This measure prevented the number of pots used being increased by the building of a larger vessel. The effect of this legislation was to reduce fishing effort from about 10^7 pot lifts in 1962/63 to about 7 x 10^6 pot lifts in 1963/64. Total catch decreased somewhat from 9.3 x 10^6 kg in 1962/63 to 8.1 x 10^6 kg in 1963/64 but subsequently recovered to about 8.7 x 10^6 kg by 1966/67. Catch per pot lift improved slightly from an average of 1.04 kg per pot lift for the 3 years prior to the introduction of the legislation to 1.09 for the 3 subsequent years. However, the most important effect was that the rapid escalation of the fishing effort of the late 1950s was halted.

Since the introduction of this limited entry policy to control fishing effort, total catches have remained stable at about 8 x 10^6 kg although because of increased efficiency of the individual operators in the industry, fishing effort had by 1974 again increased to levels similar to those immediately prior to 1962. Further reduction in fishing effort was indicated since subsequent analysis of fisheries data and application of fisheries models confirmed the concern experessed in 1962 regarding the effect on catches of high levels of fishing effort. In addition concern was expressed about the effect of this high level of effort on the reproductive potential of the stock.

The limited entry nature of the fishery, however, has posed some problems in the selection of the most suitable methods to be used to achieve further fishing effort reduction. One of these problems is the increased capitalisation

Table 1

Average catch and fishing effort for the Western Australian rock lobster fishery, 1944–1975

Year	Average catch (kg x 10^6)	Average No. pot lifts (x 10^6)	Catch per pot lift	Average No. of men employed
1944/45–1948/49....	0·994	0·618	1·608	109
1949/50–1953/54....	3·547	2·284	1·553	402
1954/55–1958/59....	5·805	4·172	1·391	734
1959/60–1963/64....	8·541	7·815	1·093	1 378
1964/65–1968/69....	8·434	7·647	1·103	1 350
1969/70–1973/74....	7·338	9·407	0·780	1 668

of the industry brought about by the fact that the fishing licence (i.e. the right to fish) has acquired a considerable monetary value. This makes the reduction of boat or pot numbers an almost prohibitively expensive exercise either for Government or industry. Alternative strategies which effect each individual equally are therefore necessary and some of the options which have been examined are changing the legal minimum size and implementing additional closed seasons. In fact a 6 week additional closure has been implemented on a trial basis for the 1977/78 season. The problems of effort reduction in a highly capitalised, limited entry fishery such as the rock lobster industry have not been fully resolved but solutions will need to be found if increasing efficiency continues to result in increasing fishing effort.

Although the Western Australian rock lobster fishery stands as one of the few examples of a well-managed fishery, those management techniques that have been chosen have themselves resulted in a new set of problems. Present research is addressing itself to the resolution of these new problems.

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The breeding seasons of birds in south-western Australia

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Abstract

Data are presented on the dates when 2 703 clutches of eggs were laid by birds breeding in south-western Australia, defined as that part of Australia west of the Western Australian border and south of 26°S latitude. In all except two species, autumn breeding was rare and irregular. Over 90% of the clutches were laid between July and December inclusive. Within that overall generalisation, some more specific trends were evident.

Most species tended to lay earlier in the inland than in the south-western corner, but the trend was reversed in two species. Species taking nectar as a food source tended to breed before those taking grain. Ground insectivores bred earlier than aerial insectivores. Raptors and water birds tended to breed later than other groups.

Consideration of data for individual species showed that although each species had a characteristic breeding period, it varied regionally and from year to year in the same place. No good correlation emerged between measurement of rainfall and temperature and the onset or duration of breeding, although these factors appeared to exercise some control in some species. Rather, it seems that the timing of the birds' breeding season relates directly to the abundance of the birds' food supply and may be controlled more by the food available for parents than by potential food availability for the young.

It is pointed out that the concentration of breeding in south-western Australia into the period from July to December implies that resources are most abundant then. As a consequence, much more serious effects on the avifauna might be expected from burning in the spring than in the autumn, because it would destroy the resources which should provide food for the birds for the following twelve months.

Introduction

The time when birds breed in south-western Australia, defined as that part of the continent south of latitude 26°S and west of the Western Australian border, has attracted attention for many years. Carnaby (1946) and Serventy (1946) noted that although birds of south-western Australia normally bred in the spring, autumn nesting was observed in some years. (The terms spring and autumn refer to the seasons as understood in the Southern Hemisphere; spring is September to November, autumn is March to May). They speculated that such out of season nesting could be caused directly by out of season rainfall (with which it had been observed to correlate) or by an increase in food supply consequent upon the rainfall.

Further observations were published by Carnaby (1954), Robinson (1955) and Sedgewick (1955) which provided abundant evidence of a spring breeding period in the far south-west and occasional autumn breeding in northern areas. Following Keast and Marshall's (1954) publication of histological evidence of gonad response to rainfall in Australian arid-zone birds, Serventy and Marshall (1957) published detailed observations of two autumn breeding episodes in south-western Australia. Their data showed that the gonads of many species enlarged after cyclonic rains in March 1953 and February 1955, that the males were stimulated more than the females, that some species naturally laid eggs and reared young in the autumns following the cyclones, and that the incidence of this autumn breeding was greater in the northern parts of south-western Australia than in the more south-westerly parts. Serventy and Marshall proposed that the occurrence of spring breeding in south-western Australia during a period of increasing day length was probably coincidental. They considered that the critical stimuli to reproduction are probably environmental conditions that arise after rainfall and with the increasing temperatures that accompany the lengthening photo-period. They pointed out that low temperatures appeared to inhibit breeding and that the amount of unseasonal breeding might be related to the degree of beneficial change to the environment that followed the rain. They considered that these effects could not be observed in all birds, notably not in sea birds, and considered the possibility that the breeding response might be generated by a sudden improvement in food supply consequent upon the rain, although

they noted that the response was more rapid than they would have expected an increase in availability of food to be.

Little more was published about the breeding seasons of birds in south-western Australia for some years until Nix (1976) in an analysis of the movements and breeding of birds in Australia and New Guinea also considered the role of food supply in the control of the timing of breeding. He simulated on a computer the growth periods of plants and showed that these occurred at different times in different parts of Australia. He suggested that the factors controlling the timing of birds' breeding seasons would regulate them to coincide with the maximum food abundance. He suggested that the breeding seasons of insectivores, nectarivores, frugivores and graminivores would succeed each other just as the stages of growth of the plants succeeded each other. Taking data from Ford and Stone, (1957) who published records of breeding from Kellerberrin, he confirmed that south-western Australian species have a major breeding season in late winter and early spring which is the period most favourable for plant growth. His model showed that a smaller episode of plant growth occurred in the autumn and noted Serventy and Marshall's (1957) observations of autumn breeding.

The results of these earlier studies have demonstrated that most breeding in birds in south-western Australia occurs in the spring, but that autumn breeding does occur sometimes, associated with unseasonal autumn rain. The authors have universally accepted that an ultimate factor controlling the timing of breeding must be the birds' food supply but the early speculation that an important proximate factor timing the breeding episode was rainfall itself has gradually lost ground in favour of the speculation that the environmental effects of the rainfall may be more important. In addition, Nix (1976) has postulated a sequence of breeding that relates to the sequence of plant growth.

Three recent studies of single species are now available and show trends in individual species more clearly. Nicholls (1964, 1974) has shown that the wild individuals of the Silver Gull, *Larus novaehollandiae,* can breed successfully in both autumn and spring of the same year, and Saunders (1977) has shown the same thing for wild individuals of the Red-tailed Black Cockatoo, *Calyptorhynchus magnificus*. Davies (1977) has shown that although Zebra Finches, *Poephila guttata,* breed mainly in the spring in the northern part of south-western Australia as defined here, they do breed in the autumn if summer rains have brought up a crop of their main food, *Aristida contorta*. In spring, successful breeding correlates with high winter body weights and therefore by implication with a good food supply rather than with heavy rainfall.

Other data presented here comes from the Nest Record Scheme of the Royal Australasian Ornithologists Union and from the records of myself and my colleagues. It confirms the trends already reported and expands the numbers of species for which details can be given so that a reasonable comparison can be made between the succession of birds breeding and the sequence of plant growth, as well as allowing further interpretation of the role of rainfall and temperature in timing the breeding episodes.

Methods and material

The collection of data in the Royal Australasian Ornithologists Union Nest Record Scheme has been examined and 1 298 cards found which provide information about the dates when birds breed in south-western Australia. Cards were only accepted if they enabled the calendar month in which eggs were in the nest to be determined. If this spanned two months, the earlier was chosen. In all cases, conservative estimates of the egg-laying and incubation period were used, for these are still unknown with respect to many Australian birds. Personal records of 163 nests with eggs at Mileura, Western Australia, have been included with the RAOU nest record data.

Data on three species, the Zebra Finch, the Yellow-rumped Thornbill, *Acanthiza chrysorrhoa,* and the Black-faced Woodswallow, *Artamus cinereus,* were obtained from the original notebooks of D. L. Serventy and relate to observations made at Grass Valley, York, from 1959 to 1963, referred to in Oksche *et al.* (1963).

Observations on Black-faced Woodswallows nesting at Manmanning, on Splendid Wrens, *Malurus splendens,* nesting at Gooseberry Hill near Perth and on the Galah, *Cacatua roseicapilla,* have been contributed by Ian Rowley, and data on the nesting of White-tailed Black Cockatoos, *Calyptorhynchus baudinii,* in the Western Australian wheatbelt, have been contributed by Denis Saunders. In all cases, records have only been accepted if the calendar month in which there were eggs in the nest could be unequivocally determined.

In the analysis of these records involving comparisons amongst them, statistical methods are difficult to use, both because nest searching cannot be considered to be non-random and because the coverage of the area under consideration is not even. For example, there are abundant records from a few centres where keen ornithologists reside such as Woodanilling, Mileura, the Nullarbor Plain and Manjimup. This problem affects all studies of when birds breed, e.g. Frith and Davies (1961) and Lavery *et al.* (1968), and it is only when the raw data show overwhelming trends that reasonable certainty can be assumed. In the present study, D. L. Serventy's data from York are of great value, for the area was visited regularly each three weeks and searched systematically for nests on each visit. The trends showing up in his results should, therefore, be free from bias due to non-random searching and provide an accurate picture of the timing of breeding of these three species in the York area.

In order to analyse regional trends within south-western Australia itself, regional boundaries used by the Commonwealth Bureau of Meteorology, in their published statistics, have

been adapted and are shown in Figure 1. The Bureau of Meteorology's south-west divisions 9 and 9A correspond to the south-west division of Figure 1; its south-west divisions 8, 10 and 10A correspond to the wheatbelt division of Figure 1 and its divisions 6 (part), 7 (part), 7A, 11, 12 and 13 (part) correspond to the inland division of Figure 1. These boundaries do not correspond exactly with mean annual isohyets as shown, for example, by Nix (1976) but are quite close to the 600 mm and 350 mm isohyets, and conveniently divide the forested south-west from the cleared wheatbelt and the arid interior.

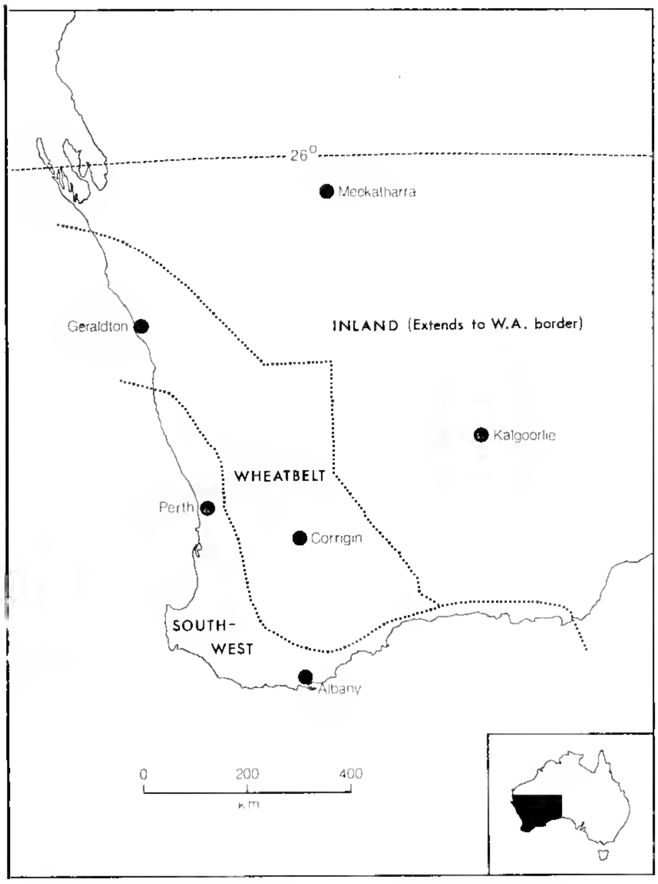

Figure 1.—Map of south-western Australia showing the three regional sub-divisions used in this paper.

Results

RAOU Nest Record Scheme and personal records from Mileura

Table 1 shows an analysis of the breeding season data available for species represented by less than 10 records. The species have been grouped by their broad ecological niche, as has become conventional in regional studies of breeding seasons (Frith and Davies 1961, Lavery *et al.* 1968). The species included under each heading are listed in Appendix I. Table 1 indicates a predominantly spring breeding season: 31% of records recorded eggs in the nest in September, 68% recorded eggs in the nest in the three spring months, and 94% recorded eggs in the nest between July and December. The sequence of nesting insectivores, nectarivores and graminivores follows that hypothesised by Nix (1976), except that aerial insectivores are considerably later than ground insectivores. Table 2 gives data for species represented by 10 to 19 records. Again there is evidence of a predominantly spring breeding season: 32% of records recorded eggs in the nest in September, 65% recorded eggs in the nest in the three spring months, and 93% of the records were of eggs in the nest between July and December. Of the individual species, those that had eggs in the nest between January and June were the aquatic Little Grebe, *Tachybaptus novaehollandiae,* and migrant Clamorous Reed Warbler, *Acrocephalus stentoreus,* both of which nested late, and a number of species in which odd individuals nested early, the White-faced Heron, *Ardea novaehollandiae* (2), Wood Duck, *Chenonetta jubata* (1), Whistling Kite, *Haliastur sphenurus* (1), Wedge-tailed Eagle, *Aquila audax* (4), Crested Pigeon, *Ocyphaps lophotes* (3), Richard's Pipit, *Anthus novaeseelandiae* (1), Black-faced Cuckoo-shrike, *Coracina novaehollandiae* (2), White-fronted Chat, *Ephthianura albifrons* (2), Australian Magpie lark, *Grallina cyanoleuca* (1), and Grey Butcherbird, *Cracticus torquatus* (1). In some cases these nests were earlier than the bulk of the population and others may best be classified as autumn nesting attempts. Tables 1 and 2 indicate a clear tendency for species of birds in south-western Australia to nest from July to December. This trend is evident even though regional differences and differences between individual years cannot be taken into account in these data.

Table 1

Breeding seasons of birds in south-western Australia (species with less than 10 records)

	J	F	M	A	M	J	J	A	S	O	N	D	Totals
Aerial Insectivores	....	....	....	....	....	....	....	1	10	4	4	3	22
Ground Insectivores....	....	....	....	1	2	1	15	28	46	29	20	4	146
Nectarivores	2	....	....	....	....	1	4	16	19	13	9	1	65
Graminivores	....	4	2	....	2	....	1	16	17	8	6	1	57
Omnivores	....	....	....	....	1	2	....	9	4	....	....	....	16
Shore and sea birds	1	....	....	....	....	....	2	4	9	4	11	4	35
Raptors	....	....	....	....	....	....	....	1	14	12	3	....	30
Water birds	3	....	....	....	....	....	....	5	5	2	10	9	34
Totals	6	4	2	1	5	4	22	80	124	72	63	22	405

Table 2

Breeding seasons of birds in south-western Australia (species with 10–19 records)

	J	F	M	A	M	J	J	A	S	O	N	D	Main data from
Little Grebe *Tachybaptus novaehollandiae*	4	2	....	....	....	....	....	....	....	3	1	4	Manjimup (8), Wooroloo (4)
White-faced Heron *Ardea novaehollandiae*	....	....	1	....	....	1	3	4	2	....	....	....	Woodanilling (5)
Mountain Duck *Tadorna tadornoides*	....	....	....	....	....	....	8	6	1	....	....	....	Woodanilling (11)
Black Duck *Anas superciliosa*	....	....	....	....	....	....	....	2	7	1	....	....	Yunderup (1), Benger (4)
Grey Teal *Anas gibberifrons*	....	....	....	....	....	....	....	2	8	2	3	....	Woodanilling (6)
Wood Duck *Chenonetta jubata*	....	....	....	....	....	....	3	2	7	1	....	1	Woodanilling (6)
Whistling Kite *Haliastur sphenurus*	....	....	....	....	....	1	....	7	....	2	....	....	Woodanilling (7)
Wedge-tailed Eagle *Aquila audax*	....	....	....	....	....	4	....	3	4	3	....	1	Mileura (9)
Brown Falcon *Falco berigora*	....	....	....	....	....	....	....	2	8	2	....	....	Nullarbor Plain (8)
Little Button-quail *Turnix velox*	....	....	....	....	....	....	....	8	2	1	1	1	Rawlinna (12)
Crested Pigeon *Ocyphaps lophotes*	....	1	2	....	....	....	....	....	5	....	3	....	Mileura (4)
Galah *Cacatua roseicapilla*	....	....	....	....	....	....	....	12	9	....	....	....	Kathleen Valley (9)
Port Lincoln Parrot *Barnardius zonarius*	....	....	....	....	....	....	....	3	5	2	....	....	Cunderdin (3), Perth (2)
Tawny Frogmouth *Podargus strigoides*	....	....	....	....	....	....	....	4	6	1	....	....	Mileura (2), Nullarbor Plain (2), Woodanilling (2)
Sacred Kingfisher *Halcyon sancta*	....	....	....	....	....	....	....	....	....	....	10	....	Katanning (3), Woodanilling (2)
Richard's Pipit *Anthus novaeseelandiae*	....	....	....	....	1	....	3	4	5	2	2	....	Woodanilling (5), Nullarbor Plain (5)
Black-faced Cuckoo-shrike *Coracina novaehollandiae*	....	....	....	1	1	....	....	3	4	5	2	1	Woodanilling (4), Nullarbor Plain (3)
Ground Cuckoo-shrike *Coracina maxima*	....	....	....	....	....	....	....	5	7	....	....	....	Nullarbor Plain (8)
White-winged Triller *Lalage sueurii*	....	....	....	....	....	....	....	....	4	4	4	1	Woodanilling (7)
Grey Shrike-thrush *Colluricincla harmonica*	....	....	....	....	....	....	1	2	6	3	....	....	Nullarbor Plain (5), Woodanilling (3)
Clamorous Reed Warbler *Acrocephalus stentoreus*	8	....	....	....	....	....	....	....	....	....	3	7	Manjimup (18)
Brown Songlark *Cinclorhampus cruralis*	....	....	....	....	....	....	9	1	....	....	....	....	Nullarbor Plain (10)
Varied Sittella *Daphoensitta chrysoptera*	....	....	....	....	....	....	....	3	2	3	2	....	Woodanilling (7)
Yellow-throated Miner *Manorina flavigula*	....	....	....	....	....	....	2	5	12	2	....	....	Woodanilling (7), Cunderdin (5)
Crimson Chat *Ephthianura tricolor*	....	....	....	....	....	....	4	2	7	....	5	....	Nullarbor Plain (14)
White-fronted Chat *Ephthianura albifrons*	....	....	....	1	....	1	7	2	....	....	....	....	Woodanilling (7)
Magpie Lark *Grallina cyanoleuca*	....	....	1	....	....	....	1	5	4	2	....	....	Woodanilling (5), Miling (3)
Masked Woodswallow *Artamus personatus*	....	....	....	....	....	....	....	4	2	1	10	....	Nullarbor Plain (10)
Dusky Woodswallow *Artamus cyanopterus*	....	....	....	....	....	....	....	....	....	8	9	1	Woodanilling (9), Manjimup (5)
Grey Butcherbird *Cracticus torquatus*	....	1	....	....	....	....	....	1	17	....	1	....	Coolup (10)
Totals	12	4	4	2	2	7	41	92	134	48	56	17	Grand total: 419

Table 3

(a)—Grouped breeding seasons—all birds with more than 20 records; summary by months

District	J	F	M	A	M	J	J	A	S	O	N	D	Totals
S.W.	1	....	....	....	1	7	4	25	33	38	21	11	141
Wheatbelt	....	1	....	2	10	6	18	31	32	30	14	6	150
Inland	....	2	15	12	20	14	31	87	127	19	37	....	364
Totals	1	3	15	14	31	27	53	143	192	87	72	17	655

(b)—*Breeding seasons grouped by districts; species with more than 20 cards*

Species	District	J	F	M	A	M	J	J	A	S	O	N	D	Totals
Willie Wagtail	SW	....	....	....	....	....	....	....	1	1	8	3	3	16
	Wheatbelt	....	....	....	....	....	....	....	....	5	10	2	2	19
	Inland	....	....	....	....	....	....	1	1	11	....	2	....	15
Red-capped Robin	Wheatbelt	....	....	....	....	....	....	....	5	6	5	5	....	21
	Inland	....	....	....	....	....	....	....	6	1	....	....	....	7
Black-faced Woodswallow	Wheatbelt	....	....	....	....	....	....	....	....	....	2	6	1	9
	Inland	....	....	....	....	....	....	....	....	13	2	6	....	21
Welcome Swallow	SW	....	....	....	....	....	....	....	8	13	9	6	....	36
	Inland	....	....	....	1	....	....	....	3	2	1	....	....	7
Silvereye	SW	1	....	....	....	....	....	....	....	5	3	2	2	13
	Wheatbelt	....	....	....	....	....	....	....	....	2	6	....	....	8
Magpie	SW	....	....	....	....	....	....	....	9	10	4	....	....	23
	Wheatbelt	....	....	....	....	....	....	....	9	7	3	....	....	19
Black Swan	Wheatbelt	....	....	....	....	....	....	2	3	2	....	....	....	7
	Inland	....	4	3	11	....	....	....	....	....	....	....	....	18
Banded Plover	Wheatbelt	....	....	....	1	4	....	6	2	2	1	....	....	16
	Inland	....	....	....	....	1	1	6	8	....	....	....	....	16
Australian Dotterel	Wheatbelt	....	1	....	1	6	2	1	1	....	....	....	....	12
	Inland	....	1	....	....	2	4	8	2	....	....	1	....	18
Coot	SW	5	....	....	....	....	....	....	....	1	4	9	9	28
Red Wattlebird	SW	....	....	....	....	1	1	1	2	6	3	....	....	14
Raven	Wheatbelt	....	....	....	....	....	4	6	6	3	....	....	....	19*
Kestrel	Inland	....	....	....	....	....	....	....	5	50	4	3	....	62
White-browed Babbler	Inland	....	....	1	3	2	1	3	3	7	....	3	....	23
Zebra Finch	Inland	....	1	10	5	2	6	7	16	13	12	22	....	94
Little Crow	Inland	....	....	....	....	....	3	6	41	26	....	....	....	76
Totals		3	15	14	29	22	47	131	186	77	70	17	6	617

*One card from the SW.

For those species represented in the records by 20 or more cards, regional differences can be examined. The data are presented in Table 3. Table 3(a) presents the grouped results: 29% recorded eggs in the nest in September, 64% recorded eggs in the nest in the three spring months, and 86% recorded eggs in the nest between July and December. Looking at regional differences, the percentage of records of eggs in the nest in September was 23, 21 and 35 for the south-west, wheatbelt and inland respectively. This was the highest percentage of any month for the inland but in the wheatbelt and south-west, the spread was more even over August, September and October and in the south-west a slightly higher percentage occurred in October (27%) although the difference is small.

The data for individual species with sufficient records for at least one region to be considered separately are shown in Table 3(b), and the trends are easier to see. The Willie Wagtail, *Rhipidura leucophyrs*, Red-capped Robin, *Petroica goodenovii*, and Black-faced Woodswallow tend to nest earlier in the inland than in either the wheatbelt or the south-west. The Australian Magpie, *Gymnorhina tibicen* and Silvereye, *Zosterops lateralis*, do not show differences between wheatbelt and south-west although the Silvereye appears to have a more extended breeding season in the south-west than the wheatbelt. On the other hand, both the Banded Plover, *Vanellus tricolor* and the Australian Dotterel, *Peltohyas australis*, tend to nest a little earlier in the wheatbelt than the inland. There are insufficient data from the other species to compare regions.

A second important phenomenon begins to emerge in Table 3. Some species characteristically breed both between January and June and between July and December whilst others breed only between July and December. Thus all the nests of the Willie Wagtail, Red-capped Robin, Black-faced Woodswallow, Australian Magpie and Nankeen Kestrel, *Falco cenchroides*, occur between July and December. A few Australian Ravens, *Corvus coronoides*, and Little Crows, *Corvus bennetti*, nested in June and one Silvereye and a few Coots, *Fulica atra*, were recorded with eggs in the nest in January, but otherwise these four species only nested between July and December. In other species some nests were recorded between January and June but in these cases there were fewer nests between January and June than between July and December. These species were (figures in parentheses compare nests in first and second half of the year): Banded Plover (7:25), Welcome Swallow, *Hirundo neoxena* (1:42), Red Wattlebird, *Anthochaera*

Table 4

Breeding seasons (number of nests with eggs) of three passerines at York over five seasons (data from D. L. Serventy)

Species/Year	No. of Visits	M	J	J	A	S	O	N	D	J	F	M	A	M	Totals	Autumn nests
Zebra Finch *Poephila guttata*—																
1959–60	14	....	....	....	....	1	11	4	....	....	1	1	4	1	23	7
1960–61	17	....	....	....	....	1	3	2	2	7	3	1	4	....	23	15
1961–62	17	....	....	....	....	....	1	6	5	2	1	....	....	....	15	3
1962–63	17	....	....	....	1	....	....	3	2	1	1	4	3	....	15	9
1963–64	18	....	....	....	....	1	2	3	....	....	3	0	1	2	12	6
Totals	....	....	....	....	1	3	17	18	9	10	9	6	12	3	88	40
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*—																
1959–60	14	....	....	....	....	2	4	1	....	....	....	....	....	....	7	....
1960–61	17	....	1	4	3	1	2	4	....	....	....	....	....	....	15	....
1961–62	17	....	....	....	2	4	3	3	....	....	....	....	....	....	12	....
1962–63	17	....	....	....	5	1	3	....	....	....	....	....	....	....	9	....
1963–64	18	1	....	1	....	....	....	....	....	....	....	....	....	....	2	....
Total	....	1	1	5	10	8	12	8	....	....	....	....	....	....	45	....
Black-faced Woodswallow *Artamus cinereus*—																
1959–60	14	....	....	....	....	....	1	1	1	1	....	....	....	....	4	1
1960–61	17	....	....	....	....	....	....	3	1	....	....	....	....	....	4	....
1961–62	17	....	....	....	....	....	1	4	4	....	....	....	....	....	9	....
1962–63	17	....	....	....	....	....	....	....	1	....	....	....	....	....	1	....
1963–64	18	....	....	....	....	....	....	....	....	....	....	....	....	....	0	....
Totals	....	....	....	....	....	....	2	8	7	1	....	....	....	....	18	1

caruncúlata (2:12), White-browed Babbler, *Pomatostomus superciliosus* (7:16) and Zebra Finch (24:70). Two species stand apart. The Australian Dotterel appears to be predominantly an autumn and winter nesting species, both in the wheatbelt and the inland and the Black Swan, *Cygnus atratus*, has been recorded nesting in the autumn in the inland and the late winter, early spring in the wheatbelt. Further data collected by Tingay *et al.* (1977) indicate that it nests in the late winter in the south-west.

Other data

Grass Valley, York.—D. L. Serventy's data are presented in Table 4 and show that each species has a characteristic breeding pattern. The Zebra Finch shows a large peak of nests with eggs in October and November, and a smaller peak in April. This resembles the data for that species shown in Table 3, but the start of intense spring nesting is earlier in the inland than in the wheatbelt at York. On the other hand, summer nests occur in the wheatbelt whereas they are rare in the inland. Most nests of the Yellow-rumped Thornbill were recorded in August, September and October and most of the Black-faced Woodswallow nests were in November and December, in agreement with the trend shown in Table 3(b) for this species to nest later in the wheatbelt than at inland sites.

Differences between years are evident. In 1959-60 and 1963-64, the Zebra Finch had well separated spring and autumn breeding seasons. In 1961-62 breeding was over in February, and the species effectively bred only in the spring. On the other hand, in 1962-63, most of the breeding was in the summer and autumn, and in 1960-61 breeding was continual from September to April.

The total monthly rainfall at York is shown in Figure 2. It is not easy to find direct correlations between rainfall and the breeding of Zebra Finches. The total nests found in the study area each season correlates positively (Spearman's $r = +0.95$; $P < 0.05$) with the total rainfall in January of the year in question, but it is not easy to accept this as a valid correlation, for in some years, e.g. 1961-62, the bulk of the nesting is over by January. There seems to be no clear association between the start or end of the winter rain period and the start of the breeding season, nor between summer rainfall and the presence of summer breeding. In Figure 2, the mean monthly temperatures recorded at Perth are shown. Although this locality is 100 km west of York, the trend shown in a comparison across years would be similar in the two sites. There is no clear correlation between temperature and the pattern of breeding shown by the Zebra Finches. It is likely, therefore, that the birds are not responding directly to these environmental factors, although the timing of breeding may be controlled by the indirect effects of environmental changes.

The same statement may be made about the breeding of the Yellow-rumped Thornbill and the Black-faced Woodswallow. In both there are differences between years but in neither do these differences relate directly to differences between rainfall and temperature patterns in the corresponding years. Yellow-rumped Thornbills bred early in 1960-61 and 1963-64 and in 1963-64 failed to breed at all in their normal spring period. In comparison with Ford's data from Bibra Lake, Perth (Ford, 1963) for some of the same years (1959 and 1961) this species bred one to two months earlier at York than on the coast. The Black-faced Woodswallows bred consistently

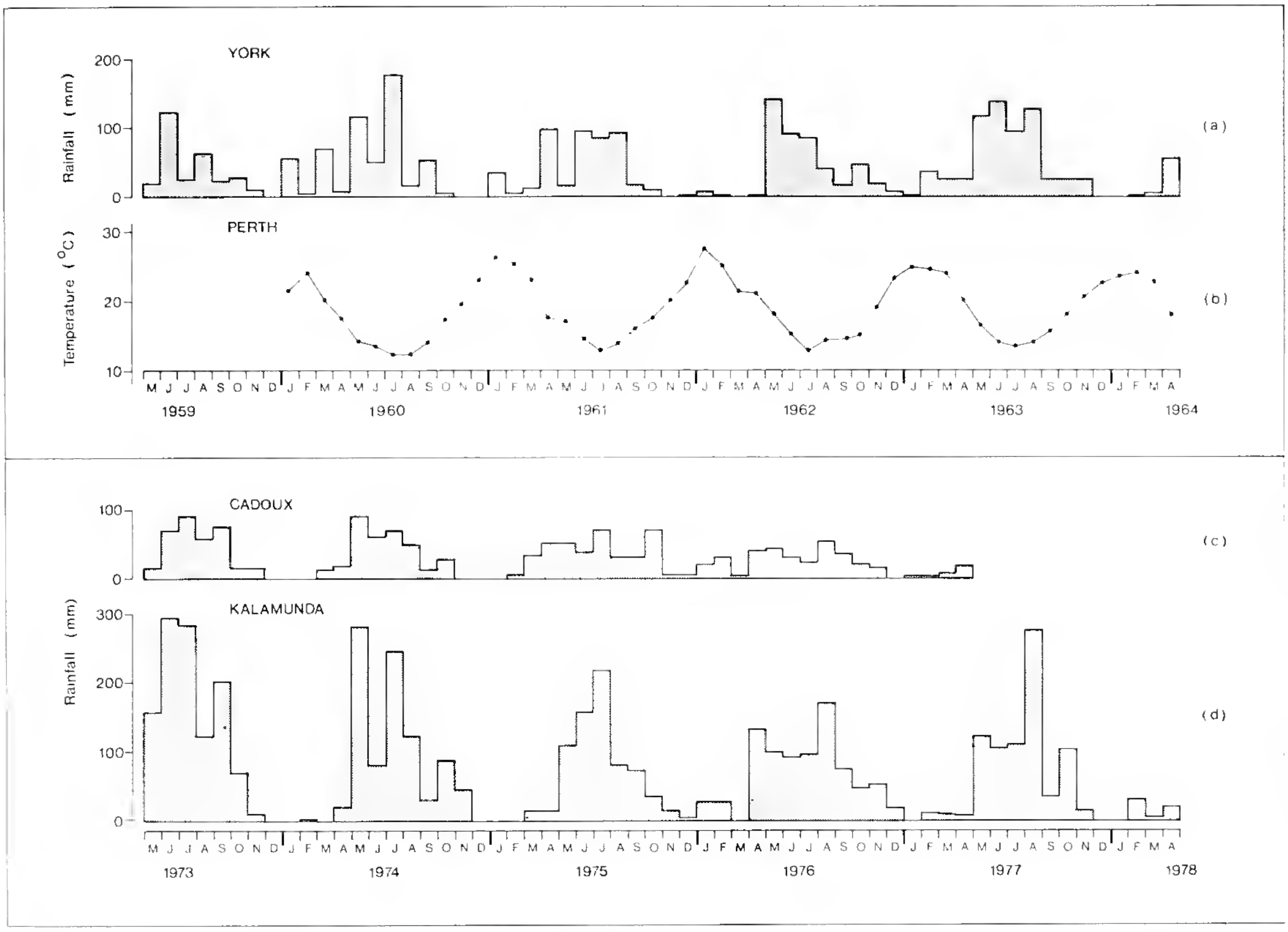

Figure 2.—Environmental data for three sites at which breeding data were collected. (a) Monthly rainfall totals for York. (b) Mean monthly temperatures for Perth. (c) Monthly rainfall totals for Cadoux. (d) Monthly rainfall totals for Kalamunda.

in late spring, early summer, but in 1962-63 and in 1963-64 only one nest was found in the study area, and breeding did not seem to have taken place.

Serventy's data, therefore, indicate that in one place, each species has a characteristic breeding time, but that the precise timing varies from year to year. Further, the changes in timing with different years do not correlate between species. Thus the Zebra Finch bred early in 1959-60 but late in 1960-61, whereas the reverse was true for the Yellow-rumped Thornbill.

Manmanning.—Rowley's data for the Black-faced Woodswallow are presented in Table 5 and show that breeding is a month earlier than for the same species at York. Again there are differences between individual years both in timing and extent of the breeding period. The mean monthly rainfall at Cadoux, 8 km north of Manmanning is shown in Figure 2. There is no clear correlation between differences in the timing and extent of the breeding season in individual years and differences in the pattern of precipitation in corresponding years.

Table 5

Breeding data from Rowley for two species of birds in south-western Australia. (Number of nests with eggs.)

Years	Month					Total
	S	O	N	D	J	
(a) Black-faced Woodswallow, Manmanning.						
1973–74	...	3	7	3	2	15
1974–75	....	8	14	3	....	25
1975–76	....	3	12	....	....	15
1976–77	....	8	4	....	...	12
Totals	....	22	37	6	2	67
(b) Splendid Wren, Gooseberry Hill, Kalamunda.						
1973–74	2	3	2	....	..	7
1974–75	1	8	3	3	1	16
1975–76		5	5	2	....	12
1976–77	7	3	1	....	..	11
1977–78	1	3	3	1	1	9
Totals	11	22	14	6	2	55

Gooseberry Hill.—Rowley's data for the Splendid Wren show large differences between years in both the timing and extent of breeding. Rainfall figures for nearby Kalamunda are presented in Figure 2 and again no correlation is evident. There is a general trend for the species to nest at the end of the wet winter, but detailed correlations do not occur.

Galah.—Rowley's data for the Galah are presented in Table 6. The data were collected at three sites, Manmanning and Coomalloo in the south-west division and Mileura in the inland division. Galahs show considerable constancy in the timing of the nesting season from year to year and region to region. Where differences between years occur, Manmanning and Coomalloo differ in the same direction. At both sites the month in which most nests were started was August in 1971 and 1974 and September in 1972 and 1973. The data from Mileura are not extensive but do indicate a concentration of nesting in the August-September period. Overall 90% of the 581 Galah nests were started in August or September.

Table 6

Breeding data from Rowley for the Galah from three sites in south-western Australia. The figures indicate the number of nests started each month

	Year	J	F	M	A	M	J	J	A	S	O	N	D	Total
Coomalloo Creek	1971	....	....	....	....	....	....	....	23	4	5	....	....	32
	1972	....	....	....	....	....	....	....	7	15	4	....	....	26
	1973	....	....	....	....	....	....	....	4	12	2	....	....	18
	1974	....	....	....	....	....	....	2	23	4	1	....	....	30
Manmanning	1971	....	....	....	....	....	....	1	68	26	8	....	....	103
	1972	....	....	....	....	....	....	....	16	67	11	....	....	94
	1973	....	....	....	....	....	....	....	43	53	14	....	....	110
	1974	....	....	....	....	....	....	....	88	28	6	....	....	122
Mileura	1971	....	....	....	....	....	....	1	14	6	2	....	....	23
	1972	....	....	....	....	....	....	....	14	2	....	....	....	16
	1974	....	....	....	....	....	....	....	5	2	....	....	....	7
Totals		....	....	....	....	....	....	4	305	219	53	....	....	581

White-tailed Black Cockatoo.—Table 7 presents Saunders data for the breeding seasons of this species at four different localities in south-western Australia. All, except Coomalloo Creek (south-west) are in the wheatbelt division of the State. Overall differences are apparent in the timing of breeding. The most northerly locality, Coomalloo Creek, is earliest even though it is in the south-west division, and the most southern locality, Moornaming, is latest, with Manmanning and Tarwonga in an intermediate position. There are differences too between individual years at each locality. Saunders (1979) discusses these differences and can find no clear correlation between environmental variables and the timing of breeding in this species.

Table 7

Breeding data from Saunders (number of nests with eggs) of the White-tailed Cockatoo in four localities in south-western Australia

	Year	M	J	J	A	S	O	N	D	J	F	M	A	Total
Coomalloo Creek	1969	....	....	3	5	1	....	....	....	....	....	....	....	9
	1970	....	....	....	10	13	5	....	....	....	....	....	....	28
	1971	....	....	15	30	9	1	....	....	....	....	....	....	55
	1972	....	....	....	25	37	3	....	....	....	....	....	....	65
	1973	....	....	4	43	19	8	....	....	....	....	....	....	74
	1974	....	....	13	37	13	11	1	....	....	....	....	....	75
	1975	....	....	10	39	23	9	1	....	....	....	....	....	82
	1976	....	....	2	27	28	7	....	....	....	....	....	....	64
	1977	....	....	....	8	31	2	....	....	....	....	....	....	41
Manmanning	1969	....	....	1	2	2	1	....	....	....	....	....	....	6
	1970	....	....	....	3	12	3	....	....	....	....	....	....	18
	1971	....	....	....	12	8	2	....	....	....	....	....	....	22
	1972	....	....	....	....	11	2	....	....	....	....	....	....	13
	1973	....	....	....	3	5	6	....	....	....	....	....	....	14
	1974	....	....	....	7	6	....	....	....	....	....	....	....	13
	1975	....	....	....	4	6	....	....	....	....	....	....	....	10
	1976	....	....	....	3	3	....	....	....	....	....	....	....	6
	1977	....	....	....	....	....	....	....	....	....	....	....	....	0
Tarwonga	1969	....	....	1	4	1	3	....	....	....	....	....	....	9
	1970	....	....	....	1	5	7	....	....	....	....	....	....	13
Moornaming	1969	....	....	....	2	4	....	....	....	....	....	....	....	6
	1970	....	....	....	....	13	2	1	....	....	....	....	....	16
Totals		....	....	49	265	250	72	3	....	....	....	....	....	639

Mileura.—Davies (1977) has presented breeding data for the Zebra Finch at this inland site which may be compared with Serventy's data from York, a wheatbelt site. The pattern of breeding exhibited by the species is similar, with breeding taking place in the spring and to a lesser extent throughout summer and autumn, but varying in its precise timing from year to year. There was some evidence that chicks raised from autumn nestings survived less well than those raised during spring nestings.

Discussion

The results presented above show that the birds of south-western Australia tend to breed between July and December, predominantly in the spring months. Within that overall generalisation, some specific trends are evident. Although many species breed only in the spring, some also exhibit autumn breeding activities, as discussed at length by Serventy and Marshall (1957). In most cases these autumn breeding episodes are quantitatively smaller than the equivalent spring ones, but for the Australian Dotterel throughout the region, and the Black Swan in the inland, autumn breeding appears to be the dominant pattern. Regional trends also appear. In general, species breed earlier inland than in the wheatbelt or south-west. The two plovers are interesting, however, in that both breed earlier in the wheatbelt than the inland and the northern populations of White-tailed Black Cockatoos breed earlier than the southern ones.

Clear variations in the timing of breeding for individual species from year to year, suggest that photoperiod itself is not always a major determinant. Serventy and Marshall (1957) have already stressed this point. They consider that the critical stimuli to reproduction are probably environmental conditions that arise after rainfall and with relatively high temperatures that accompany the lengthening photoperiod. They also considered low temperatures to be important as a breeding inhibitor.

South-western Australia experiences a winter rainfall climate in which heavy rain is rare between November and March. The trend of south-western species to breed between July and December is, therefore, consistent with Serventy and Marshall's hypothesis, for in most years the spring is the only period following heavy rain that is also warm. Such a general hypothesis cannot be expected to apply to all species and the White-browed Babbler, Banded Plover and Australian Dotterel all nest in the winter, a cold wet period. Probably these ground-feeding insectivorous birds find food with difficulty in dry weather, but with much greater ease as the insects become active after rain. They may, therefore, be responding either to the rain, or the environmental effects of it or simply to the increased food supply.

The year to year variation in the detailed data given for the Zebra Finch, Yellow-rumped Thornbill, Black-faced Woodswallow, Splendid Wren, Galah and White-tailed Black Cockatoo show that each species must be considered separately in relation to environmental factors and that no simple relationships are evident between rainfall and breeding response.

Marshall (1961) reviews work that suggests that the timing of breeding episodes is correlated with ensuring a good food supply for the young. Much of the work up to that time sought to establish correlations between the onset of breeding and environmental variables that might precede such abundant food supplies for the young, although they may not themselves be causally related to increasing this food supply. More recently, Perrins (1970) discussed the role of food in the timing of breeding and concluded that the evidence, although not yet overwhelming, was tending to implicate the food supply of adults, particularly of the females, as an important proximate factor controlling the onset of birds' breeding. Recent work by Jones and Ward (1976) on the Red-billed Quelea, *Quelea quelea*, suggests that its breeding episodes may be timed more precisely by direct relationships between the present food supply for potential parents rather than the future food supply for young.

Some of the detailed studies of breeding in south-western Australian birds that have been published, show correlations between good supplies of food for the parents and breeding episodes. Nicholls' (1964, 1974) studies of the timing of breeding of the Silver Gull showed that there are eggs continuously on Carnac Island, off Perth, throughout the autumn, winter and spring, with little egg-laying in the winter. Very little laying occurs in summer. The food supplies of Silver Gulls in metropolitan Perth come largely from the suburban rubbish tips and offal sites adjacent to slaughter yards. These are available throughout the year. Studies by Nicholls of captive gulls showed that young chicks hatched in the summer died of heat, and if this effect operated in the wild, as it almost certainly does, there would be strong selection against gulls breeding in the summer, because energy would be wasted in a regularly unsuccessful breeding attempt. Silver Gulls, therefore, breed throughout that part of the year when chicks will survive. They have a nearly constant, plentiful food supply and the lack of winter egg-laying is probably a consequence of the nearly simultaneous start of breeding by gulls in April-May, that involves them in parental duties for the next three months. The only winter eggs would come from second breeding attempts by failed breeders.

Saunders (1977) studying the Red-tailed Black Cockatoo, showed that it bred in both spring and autumn. This species has taken to eating the fruits of an introduced weed, *Emex australis*, almost exclusively and the double breeding season may also reflect an abundant and constant food supply.

At Mileura, Davies (1977) was able to show that Zebra Finches bred in warm periods, especially the spring, in years of effective summer rainfall when the birds' food supply of grass had germinated, established and seeded well. In three years studied there was little successful breeding in one year and much successful breeding in two.

In the year of little breeding the birds' winter weights were lower than in the other two years, suggesting that the condition of the parents may be a factor determining whether or not breeding occurs. The Zebra Finch definitely did not respond by breeding after any rainy episode. The young hatched in the autumn appeared not to survive as well as those hatched in the spring, and from an evolutionary point of view may seem unimportant. On the other hand, Zebra Finch populations sustain great fluctuations, and potentially have a very high rate of increase, so that the survival of even a few birds might, in certain years, make the difference between the survival and recovery of the local population, or its total extinction. In such circumstances even a small autumn breeding episode could be important in giving a depleted population additional recruits for a spring-breeding period.

The Willie Wagtail (Table 3(b)) and Black-faced Woodswallow (Tables 3(b) and 4) are both aerial insectivores and tend to breed later than the ground insectivores, the Yellow-rumped Thornbill (Table 4) and the Red-capped Robin (Table 3(b)). This appears to correlate well with the activity of their prey, for whereas ground-dwelling insects become active as the soil wets with the first rains, the flying insects are not abundant until the weather warms up and the growth and resting stages metamorphose and begin flying. The aerial insectivores are correspondingly later in breeding than the ground insectivores. Detailed studies of individual species are needed to resolve this issue.

An interesting case is the White-tailed Black Cockatoo (Table 5) which lays early in the spring. It feeds on the fruits of Proteaceae which are available at that time. However, a second factor probably operates here, for the bird has a very long incubation and nestling period (Saunders pers. comm. 1978). Young are sometimes desiccated by the heat of summer if they have not left the nest by the end of November, and there would be in these cockatoos, as in the seagulls, strong selective pressures against starting nesting attempts late in the year. It is important to view this restraint in perspective for the distribution of these cockatoos is probably limited to areas where there is sufficient food available early in the year for them to start nesting in time to get the young out of the nest before the hot weather begins.

A clear assessment of the importance of the role of parental food supply as opposed to environmental variables in timing the initiation of breeding episodes of south-western Australian birds must await more data and preferably experimental work for which there is now ample field information to ensure unequivocal experimental design. Nonetheless one important conclusion can be drawn from this survey. The breeding seasons of south-western Australian birds are concentrated between July and December and occur particularly in the spring. Because there seems to be a clear correlation between the time birds breed and an abundant food supply, either for parents or young, it follows that the food resources on which these birds depend are particularly abundant then, and this abundance also provides a store on which they will draw for the rest of the year. If this store is destroyed, as it would be by burning off in the spring, not only will their breeding effort be jeopardised, but their store of future food will also be damaged. Although Christensen and Kimber (1975) have found that bird populations are not greatly disturbed by burning, it is clear from the present review that spring burning must be much more damaging than autumn burning. Further, as many birds feed on invertebrates, at least part of this food store must represent a peak of abundance of invertebate life, so that burning in the spring would damage the productivity and perhaps the variety of the invertebrate fauna even more severely than it would bird populations.

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Appendix I

Raptors

Osprey	*Pandion haliaetus*
Black-shouldered Kite	*Elanus notatus*
Brown Goshawk	*Accipiter fasciatus*
Collared Sparrowhawk	*Accipiter cirrhocephalus*
Wedge-tailed Eagle	*Aquila audax*
Little Eagle	*Hieraaetus morphnoides*
Spotted Harrier	*Circus assimilis*
Swamp Harrier	*Circus aeruginosus*
Peregrine Falcon	*Falco peregrinus*
Spotted Owl	*Ninox novaeseelandiae*
Barn Owl	*Tyto alba*
Kookaburra	*Dacelo novaeguineae*

Aerial insectivores

Tawny Frogmouth	*Podargus strigoides*
Owlet-nightjar	*Aegotheles cristatus*
Spotted Nightjar	*Caprimulgus guttatus*
Rainbow Bee-eater	*Merops ornatus*
White-backed Swallow	*Cheramoeca leucosternum*
Tree Martin	*Cecropis nigricans*
Fairy Martin	*Cecropis ariel*
Little Woodswallow	*Artamus minor*

Ground insectivores

Bush Stone-curlew	*Burhinus magnirostris*
Pallid Cuckoo	*Cuculus pallidus*
Black-eared Cuckoo	*Chrysococcyx osculans*
Rufous-tailed Bronze-cuckoo	*Chrysococcyx basalis*
Shining Bronze-cuckoo	*Chrysococcyx lucidus*
Southern Scrub-robin	*Drymodes brunneopygia*
Scarlet Robin	*Petroica multicolor*
Hooded Robin	*Melanodryas cucullata*
White-breasted Robin	*Eopsaltria georgiana*
Western Yellow Robin	*Eopsaltria griseogularis*
Jacky Winter	*Microeca leucophaea*
Crested Shrike-tit	*Falcunculus frontatus*
Gilbert Whistler	*Pachycephala inornata*
Golden Whistler	*Pachycephala pectoralis*
Rufous Whistler	*Pachycephala rufiventris*
Crested Bellbird	*Oreoica gutturalis*
Restless Flycatcher	*Myiagra inquieta*
Cinnamon Quail-thrush	*Cinclosoma cinnamomeum*
Nullarbor Quail-thrush	*Cinclosoma alisteri*
Grey-crowned Babbler	*Pomatostomus temporalis*
Little Grassbird	*Megalurus gramineus*
Splendid Wren	*Malurus splendens*
Red-winged Wren	*Malurus elegans*
White-winged Wren	*Malurus leucopterus*
Rufous-crowned Emu-wren	*Stipiturus ruficeps*
White-browed Scrubwren	*Sericornis frontalis*
Redthroat	*Sericornis brunneus*
Weebill	*Smicrornis brevirostris*
Western Warbler	*Gerygone fusca*
Broad-tailed Thornbill	*Acanthiza apicalis*
Chestnut-rumped Thornbill	*Acanthiza uropygialis*
Samphire Thornbill	*Acanthiza iredalei*
Southern Whiteface	*Aphelocephala leucopsis*
White-browed Treecreeper	*Climacteris affinis*
Rufous Treecreeper	*Climacteris rufa*
Striated Pardalote	*Pardalotus striatus*

Omnivores

Emu	*Dromaius novaehollandiae*
Spotted Bowerbird	*Chlamydera maculata*
Pied Butcherbird	*Cracticus nigrogularis*
Grey Currawong	*Strepera versicolor*
Torresian Crow	*Corvus orru*

Graminivores

Stubble Quail	*Coturnix pectoralis*
Painted Button-quail	*Turnix varia*
Laughing Dove	*Streptopelia senegalensis*
Diamond Dove	*Geopelia cuneata*
Common Bronzewing	*Phaps chalcoptera*
Crested Pigeon	*Ocyphaps lophotes*
White-tailed Black Cockatoo	*Calyptorhynchus baudinii*
Regent Parrot	*Polytelis anthopeplus*
Budgerygah	*Melopsittacus undulatus*
Red-capped Parrot	*Purpureicephalus spurius*
Western Rosella	*Platycercus icterotis*
Many-coloured Parrot	*Psephotus varius*
Blue Bonnet	*Northiella haematogaster*
Bourke's Parrot	*Neophema bourkii*
Elegant Parrot	*Neophema elegans*
Painted Firetail	*Emblema picta*

Nectarivores

Purple-crowned Lorikeet	*Glossopsitta porphyrocephala*
Little Wattlebird	*Anthochaera chrysoptera*
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*
Singing Honeyeater	*Lichenostomus virescens*
Purple-gaped Honeyeater	*Lichenostomus cratitius*
Yellow-plumed Honeyeater	*Lichenostomus ornatus*
Grey-fronted Honeyeater	*Lichenostomus plumulus*
White-plumed Honeyeater	*Lichenostomus penicillatus*
Brown-headed Honeyeater	*Melithreptus brevirostris*
White-naped Honeyeater	*Melithreptus lunatus*
Brown Honeyeater	*Lichmera indistincta*
New Holland Honeyeater	*Phylidonyris novaehollandiae*
White-cheeked Honeyeater	*Phylidonyris nigra*
White-fronted Honeyeater	*Phylidonyris albifrons*
Tawny-crowned Honeyeater	*Phylidonyris melanops*
Western Spinebill	*Acanthorhynchus superciliosus*
Pied Honeyeater	*Certhionyx variegatus*

Waterbirds

Great Crested Grebe	*Podiceps cristatus*
Hoary-headed Grebe	*Poliocephalus poliocephalus*
Darter	*Anhinga melanogaster*
Little Pied Cormorant	*Phalacrocorax melanoleucos*
Black Cormorant	*Phalacrocorax carbo*
Little Black Cormorant	*Phalacrocorax sulcirostris*
White-necked Heron	*Ardea pacifica*
Large Egret	*Egretta alba*
Nankeen Night-heron	*Nycticorax caledonicus*
Freckled Duck	*Stictonetta naevosa*
White-eyed Duck	*Aythya australis*
Musk Duck	*Biziura lobata*
Black-tailed Native-hen	*Gallinula ventralis*
Dusky Moorhen	*Gallinula tenebrosa*
Swamphen	*Porphyrio porphyrio*

Shore and sea birds

Little Penguin	*Eudyptula minor*
Australian Pelican	*Pelecanus conspicillatus*
Black-faced Cormorant	*Phalacrocorax fuscescens*
Pied Oystercatcher	*Haematopus ostralegus*
Hooded Dotterel	*Charadrius rubricollis*
Black-fronted Dotterel	*Charadrius melanops*
Silver Gull	*Larus novaehollandiae*
Caspian Tern	*Hydroprogne caspia*
Roseate Tern	*Sterna dougalii*
Bridled Tern	*Sterna anaethetus*
Crested Tern	*Sterna bergii*

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Niche theory and macropodid nutrition

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Abstract

Arid zones are universally acknowledged to be nutritionally hostile environments; this paper sets out to explain the observed capacities of the "ruminant-like" macropodid marsupials to survive in such environments by relating their nutritional biology to the concept of the niche. New insights are achieved by this approach. The nutritional niche is defined as a subset of the Hutchinson niche space; it is shown that the symbiotic interaction between the pregastric microbes and the host mammal enables the host to occupy an expanded nutritional niche. It is predicted that under specific and well-defined conditions, mammals with pregastric fermentation (PGF—i.e. ruminant and ruminant-like species) are competitively inferior to non-PGF herbivores in a nutritional sense, but they avoid the consequences of this competition by occupying expanded nutritional niches which exclude competitors. This nutritional theme of niche expansion common to all mammals with PGF is shown to be nutritionally flexible allowing specialization in the nutritional niche which is more pronounced than external morphology would indicate.

Introduction

Humans in arid conditions are impressed by the heat, shortage of water, and absence of shade, and it is natural to believe that arid-zone animals occur where they do because they can handle these stresses. We therefore tend to concentrate our studies on measuring the performance of arid-zone animals under laboratory conditions which are believed to represent in some way field conditions in arid places.

These laboratory studies measure achievement of animals, i.e., what the animal can endure, because when we set up laboratory experiments we take care that the animal cannot behaviourally avoid the conditions we wish to impose on it. The results of these studies are thus measures of survival, but frequently we have no measure of whether the animal experiences such conditions in the field or not.

However, in order to persist, a species must not only endure environmental stresses but also maintain a population, and this is done only when offspring survive and grow to reproductive age. Even this is not sufficient to ensure persistence, because an organism also has to contend with competitors for resources which may be in short supply. Thus three stages are involved: (a) Survival, in which physiological performance may be important but behavioural avoidance may be equally important; (b) Growth, in which nutrition, especially dietary protein, vitamins, essential lipids, minerals and energy, are important; (c) Reproductive success (also dependent on adequate nutrition), which ensures that aging animals are replaced by offspring. These stages are not equally easy to analyse. The first has fewer difficulties and is commonly studied as environmental physiology or ecophysiology. It is generally assumed that the present capacities of animals to maintain life in the face of hot arid conditions represent the culmination of all the selection there has been over the period that has elapsed since the environment became arid.

It is now thought that the onset of aridity occurred much earlier than formerly believed. It appears that a trend towards aridity started in Late Miocene times (Bowler 1976), and was accentuated by climatic oscillations of wet and dry periods in the Quaternary. Associated with these oscillations there is a well-documented extinction of many large marsupials and in those cases where extinction did not occur, selection for smaller-sized species occurred (Bartholomai 1972, 1975; Marshall 1973); but even the smaller forms have continued to disappear as, for example, potoroos were only taken shortly after the settlement of Western Australia and not subsequently. Thus it would appear that although a number of species have become rare or extinct because of European settlement, evidence from fossil and subfossil deposits implies that at the time of the colonisation of Western Australia, the faunal assemblage represented a terminal stage of a long process of extinction and a reduction of faunal diversity which began much earlier.

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It is a common observation that when faunal diversity is reduced, the surviving species frequently expand their range or occupy habitats in which they were formerly never found; ecologists describe such situations as competitive release or expansion of the realised niche. For example, the habitat occupied by the quokka *Setonix brachyurus* on Rottnest Island, and the tammar wallaby *Macropus eugenii* on the Abrolhos, is quite unlike the preferred situation on the mainland; both cases seem to indicate habitat expansion made possible in part by the absence of competitors. Another example of ecological release from constraining environmental variables has been observed in the case of kangaroos, as when pastoral water and improved grazing conditions enable kangaroos to increase in numbers (Ealey 1962, 1967; Newsome 1975). But these are exceptions because, in general, there is little evidence to suggest that range expansion has occurred in the case of the surviving fauna, and on this basis we can infer that the present depauperate fauna exists in competitive equilibrium for environmental resources.

We are still left with the question as to why so many species became extinct. And can we, by studying the ability of the faunal elements which survived the extinction, make any statement as to why the current fauna persisted? Was it physiological capacity, reproductive efficiency, nutritional flexibility or behavioural avoidance?

Some of these aspects have been previously dealt with by Main (1968, 1970, 1976, 1978) and Main and Bakker (in press). Here we propose to deal with the physiology of nutrition insofar as this has relevance to the trend to aridity already discussed. We will argue that the dominant herbivorous marsupials—the macropodids, i.e., kangaroos, wallabies, rat kangaroos—have evolved a flexible system of alimentation appropriate to the arid zone which has a recognisable nutritional theme. Moreover, we will attempt to show that this flexible nutritional theme has many variations which have been moulded by competitive interactions as predicted by ecological concepts and the theory of the niche. Finally, we will also attempt to show that the nutritional adaptations displayed by the macropodids have compromised their energetic and reproductive efficiencies.

Accordingly, this paper will not be a literature review of the physiology of desert animals as this subject has been more than adequately covered by recent reviews (Brown 1974, Russell 1974). Instead we propose to introduce a new approach to the nutritional physiology of the macropodid marsupials and then to discuss some of the biological implications of this approach. We will begin our account by introducing some basic concepts of niche theory.

The niche: an abstractly inhabited hypervolume

Niche is a term that was first used to indieate the role or function of a species in the community. The concept was not well defined, and as a result usage was not precise and the term became almost meaningless. In 1957, the concept of niche acquired elements of mathematical rigour and precision previously unrealised, due to the efforts of G. E. Hutchinson (1957) who conceived of a new way of defining the niche.

In set-theoretic terms, the fundamental niche (N) of a given species is a n-dimensional hypervolume or space. Hutchinson considered all of the environmental and biological factors (not ncessarily independent) that affect the survival of a species, and to every variable or factor he assigned an axis. On each axis he specified arbitrary limits, the limits denoting a region within which a given species can survive and persist.

To illustrate Hutchinson's concept, we will consider two familiar variables that affect the survival of desert herbivores—temperature and available water in plant tissues. A given species will survive and reproduce within a certain range of temperature and water concentration in plant tissues. If these ranges are linearly ordered on a pair of rectangular co-ordinate axes (Fig. 1A), a region (in 2 space) is defined within which the species can persist. In effect we have specified the physiological tolerances of a given species with respect to temperature and available plant water. The concept is generalised by considering all relevant variables, i.e., a third axis would define a volume or 3 space; n-axes would define a hypervolume of n-space and thus a species' *fundamental niche*.

Upon defining the fundamental niche, Hutchinson proceeded to qualify the concept by considering biological interactions (e.g. competition) among organisms. He reasoned that because of biological interactions, a species need not exist within the full extent of its fundamental niche; this contracted niche space, Hutchinson termed the *realised niche*.

An assumption, indeed a biological axiom, states that at equilibrium, no two sympatric species can occupy the same niche space. This assumption is based on the competitive-exclusion principle (see Hardin 1960); we will have occasion to invoke this principle as some important predictions flow from it.

On considering the foregoing, a little reflection reveals that much of the physiological literature represents efforts by physiologists to define a species' fundamental niche. Any studies that characterise a species' tolerance or requirement for an environmental factor can be interpreted as characterising axes or subspaces of a species' fundamental niche. Furthermore, if a physiological adaptation increases the tolerance of an organism to a stressful factor, or lowers the requirement for an environmental variable, then such adaptations may be defined as expanding the fundamental niche. We suggest that this is a useful way of describing the biological significance of physiological adaptations.

The merits of this approach will be particularly apparent when we discuss the biological implications of macropodid nutrition, as some new insights have been gained by applying the above ecological concepts. However, before we do this it will be necessary to describe some background material.

Early studies on marsupial nutrition

Pioneering studies on macropodid nutrition began when H. Waring approached R. Moir and M. Somers of the Institute of Agriculture about the nutritional significance of the unusually large forestomach of the Rottnest quokka (*Setonix brachyurus*). Their studies revealed that the quokka was "ruminant-like". Bacteria were present in huge numbers in the stomach contents and microbial end-products—volatile fatty acids (VFA)—were found in concentrations comparable to those in domestic ruminants (Moir *et al.* 1956). Subsequent work has amply confirmed their original conclusions, and the ruminant-like physiological convergence has since been extended to other macropodids as well as some eutherians (Moir 1968).

Additional nutritional studies were stimulated by Ealey's (1962, 1967) investigations on the euro or hill kangaroo (*Macropus robustus*) in the Pilbara. This work was initiated in response to the demands of pastoralists to control the euro which was viewed by the industry as a serious economic pest. One of the results of Ealey's research was the finding that pastoral watering points had enabled the euro population to increase. Under natural conditions, the euro population is limited by intraspecific competition for heat refuges in the form of caves in breakaway country—a necessary requirement to maintain water balance. By making free water readily available, the pastoral industry had removed a limiting environmental factor of the niche space of the euro; water balance could be maintained in the absence of heat refuges.

It is significant that the euro population had expanded its realised niche by interacting with a dimension (water) of an agro-ecosystem. Thus the euro is not adapted to the extreme heat as for example are some African gazelles (Taylor 1972) which have expanded their fundamental niches in a physiological way. Survival of the euro under natural conditions is achieved by appropriate behavioural responses in suitable habitats—a tactic which many animals of the arid zone employ.

While there appeared to be no unusual physiological adaptations by the euro to water, studies of their dietary preferences implicated physiology (Storr 1968). Euros were maintaining their numbers on an extremely fibrous low-protein food source (e.g. *Triodia* sp.) which did not support domestic sheep. How the euro population was adapted to such a low-grade nutritional environment remained unknown until G. Brown investigated the problem. His findings were quite remarkable, and his thesis represents a study that was the first of its kind in the sense that no-one had ever determined the nitrogen requirement of a wild species.

The remarkable results obtained from nitrogen-balance trials in the euro revealed the minimum nitrogen requirement of the euro to be 50% lower than that of sheep. The results were fully consistent with the field observations on the diet of the euro, i.e., the euro is physiologically adapted to low protein diets; it has expanded its niche space by having a low requirement for environmental nitrogen (Brown 1964, Brown and Main 1967, Brown 1969).

Perhaps equally as significant was Brown's explanation for the low nitrogen requirement of the euro. He correctly hypothesised that the euro must have a lower standard metabolism, and that the euro recycled urinary nitrogen. Two types of niche expansion are therefore responsible for the lower nitrogen requirement—the first is an expansion of the fundamental niche made possible by a lower rate of metabolism; the second is an interaction of the animal with its stomach micro-organisms, but this represents an expansion of the realised niche. The distinction is a subtle one which has not been recognised, nor have the consequences been appreciated.

Niche theory and macropodid nutrition

The arid zone is not only noted for its heat and water stresses, but also is characterised by cyclic and unpredictable bursts of primary production followed by long periods of low productivity. During these unproductive periods the standing crop may still be extensive, but the vegetation becomes nutritionally hostile, for one routinely observes in the case of macropods, a loss of body condition (Kinnear and Main 1975) and sometimes heavy mortality in the population (Ealey 1962, Main 1970).

Herbivorous mammals have never directly solved the nutritional challenge of the arid zone. They survive and persist because they have entered into a complex biological association (symbiosis) with microbes. It is significant that they have largely adapted their physiology to maintain the association and to exploit its benefits.

The associations follow two basic patterns: microbes are housed and continuously cultured in two distinct regions of the alimentary tract—either the hindgut (i.e., post-ileo) or both hindgut and foregut. In the latter case, the foregut population is invariably dominant in terms of microbial numbers and gut volume. This design of housing microbial populations in the foregut has been described as pregastric fermentation (PGF) (Moir 1965, 1968), a useful term which rigorously distinguishes PGF mammals from those species that house microbial populations solely in the hindgut (e.g. lagomorphs, perissodactyls).

PGF mammals are represented principally by ruminants and, in the case of marsupials, by the macropodids which are also referred to as being "ruminant-like". Both groups underwent an explosive radiation during middle/late Tertiary times. These evolutionary events, which occurred independently, are correlated with climatic changes that caused seasonal or discontinuous periods in primary production. It is thus a common nutritional solution, and a global phenomenon, with many variations on a theme.

The biology of this nutritional theme of housing a microbial fermentation system in the foregut has in our view never been adequately

explained nor the purpose understood. This is so despite intensive research by nutritional physiologists and animal scientists; it is generally believed that PGF is primarily an adaptation which enables the host animal to exploit fibrous (cellulosic) plant structures as a source of energy.

The rumen and its microbes are also acknowledged to have the properties of an ecosystem. Some attempts have been made to analyse the system as such, but these attempts have not yielded any fresh insights. However, new insights and properties emerge when this biological association is interpreted in terms of niche theory.

The nutritional niche

The generality of Hutchinson's fundamental niche concept allows one to partition the fundamental niche into subsets of axes. We define the *fundamental nutritional niche* as a subset of axes restricted to those axes representing nutrient variables (e.g., essential amino acids, carbon, phosphorus, essential lipids, vitamins, H_2O, etc.) essential to the persistence of a species.

It follows from the above that, if a species is to occupy a niche, there has to be a correspondence between a species' nutrient requirement (NR) and its nutritional niche space (NNS). In abstract terms this means a species must be able to map its NR set into an NNS set. If a species cannot perform this mapping then in concrete terms its nutrient source is lacking in nutrition in one or more ways; persistence is therefore not possible.

Competition, niche and PGF

A species may be capable of mapping its nutritional requirements into a nutritional niche space, but it can be prevented from occupying a niche space by more efficient competitors. This leads us to examine the competitive abilities of mammals with PGF; we will first consider the theoretical aspects and then we will review the available evidence.

The events that occur in the pregastric diverticulae are usually referred to as "digestion", but this is clearly an inappropriate word; a more accurate description of the processes that occur is *decomposition*. Food of PGF mammals is not initially digested, but is partially decomposed (to varying degrees) by microbes; associated with these events are the growth and maintenance of a microbial population—the pregastric culture.

One of the consequences of microbial decomposition is that some of the dietary components are rendered digestible (e.g. fibre) while other components can be improved in nutritive value (e.g. the essential amino-N and vitamin content); on the debit side, decomposition, as the term implies, leads to energy losses and mineralisation of the host's food. It is for these reasons that we observe the presence of the decomposition products—NH_4, H_2S, CH_4 and CO_2—in the stomach diverticulae.

To emphasise the above, we can say that ruminants and their analogues do not initially digest their food—they rot it, or at least a major part of it. In order to achieve this, these mammals have domesticated microbes and as a consequence they have acquired a unique trophic level (Kinnear and Main 1975).

In acquiring a microbial trophic level PGF mammals have increased the links in their food chain. We recognise: plants → bacteria → protozoa (if present) → mammal. If this were all we knew about these animals, we could still confidently predict on the basis of trophic energetics (and thermodynamics) that macropodids, ruminants, etc., could not possibly be as productive as non-ruminant animals. This is to be expected because productivity calculations must reckon with an additional trophic level, and the inevitable losses associated with the energy and material transfer between trophic levels. The losses are not as great as that observed in more conventional food chains because of the anaerobic (fermentative) properties of the microbial trophic level; nonetheless, as we will show, the losses are still appreciable.

Our trophic analysis has led us to predict that ruminants and their analogues are comparatively inefficient at transforming food into animal biomass. This conclusion is consistent with the experimental evidence—indeed it is an acknowledged fact in the field of animal production (Reid 1970). For example, Armstrong and Blaxter (1961) demonstrated that carbohydrate yields 11 to 30% more energy for production when digested post-ruminally than when decomposed in the rumen. Similar results occur with regard to protein utilization by ruminants. In reviewing this aspect, Smith (1975) concludes: "It seems that the degradation of food protein in the rumen and the use of the products for the synthesis of microbial protein (even though this may be of high biological value) is a very inefficient and wasteful means of using protein resources." In recognition of these inefficiencies it is not surprising therefore to note that animal scientists are endeavouring to develop feeding regimens which enable the rumen microbes to be bypassed (Owens and Isaacson 1977).

To summarise our discussion to this point, we have shown that PGF mammals are relatively inefficient in converting food resources into animal biomass. But this conclusion makes one uneasy for it seems to create a paradox. Given that PGF mammals suffer from measurable inefficiencies, how can we explain the success of the group? What has happened must be this: these animals have made energetic and nutritional compromises in exchange for the ability to exploit and colonise niches that nutritionally exclude most other mammals with different alimentary systems; in other words, they do not compete with non-PGF herbivores for the same sort of food.

The nutritional niche space of mammals with PGF

Since we have reached the conclusion that PGF mammals cannot compete with non-PGF herbivores, we have raised the question—What is their nutritional niche?

Now the symbiosis between the microbial trophic level and the host animal is a biological interaction, and according to Hutchinson (1957) biological interactions affect the dimensions of the niche hypervolume. Competition is known to contract the niche hypervolume while the converse—symbiosis, which is really negative competition—should therefore expand the niche space. Thus mammals with PGF should be capable of occupying expanded niches. Again the literature supports our predictions—consider the following evidence.

Nutritional niche expansion means that an organism can lower its requirement for a nutrient or increase its tolerance to excess of a nutrient or both. There are many examples of this in the ruminant literature, and perhaps the most impressive examples are the demonstrations which show that domestic ruminants can be maintained in a healthy and productive state when fed diets containing non-protein nitrogen (NPN) as a sole replacement for protein N. Virtanen's (1967) long-term feeding trials with high-yielding milk cows are outstanding examples of a ruminant's ability to eat foods deficient in essential nutrients, i.e. essential amino acids, water-soluble vitamins and essential lipids. With regard to other ruminant-like mammals little work has been done, but Brown (1964, 1969) replaced part of the protein N with urea N (30% of N intake) and kangaroos maintained N-balance. The evidence for the recycling of N by camels (Schmidt-Nielsen *et al.* 1957) and by wallabies (Kinnear and Main 1975) is indicative of NPN utilisation. Recycling of N, of course, is another example of niche expansion —it lowers the environmental nitrogen requirements of an animal.

We have so far focused our discussion on essential nutrients, pointing out that the pregastric microbial/mammal symbiosis has resulted in niche expansion by eliminating the need for an array of essential nutrients. But mammals with PGF can also use microbes to detoxify plant poisons (e.g. oxalates, alkaloids; Freeland and Janzen 1974), which also results in niche expansion because the microbes have extended the host's tolerances to toxic substances in the food.

It should be stressed that the foregut symbiosis has expanded the realised nutritional niche, and has not affected the host's fundamental nutritional niche. Ruminants still require a full array of preformed essential nutrients; without their pregastric microbes they would require a balanced diet complete in all respects.

Evidence for nutritional niche expansion

Nutritional niche expansion means that under natural conditions, PGF mammals should be eating foods that are unnutritious in one or more ways. The evidence supporting this prediction is sparse for the simple reason that dietary studies on wild herbivores have been limited to what an animal eats, and occasionally to the gross chemical composition of the diet, e.g. nitrogen, lipids, fibre, minerals, etc. What is necessary to prove our predictions are dietary analyses which measure the essential amino acids, vitamins, essential lipids and toxic substances in an animal's natural diet.

Unfortunately, these analyses are difficult to perform, for they require sophisticated equipment and technical expertise; furthermore, there are also technical difficulties in the field because it is difficult in most instances to define what plants a herbivore is eating, the amounts consumed, as well as the digestibility. In view of this situation, what seemed obviously necessary to us was to find a ruminant-like animal with simple well-defined dietary habits. We were fortunate in finding such an animal in the woylie or brush-tailed rat kangaroo *(Bettongia penicillata)*.

In a study of the ecology of woylies near Manjimup, Western Australia, P. Christensen (1977) discovered that woylies dig up and eat small pebble-sized fungi. We also discovered from stomach content analyses that woylies were eating a gum exudate from the trunk of *Hakea* sp. There was no evidence that woylies were eating green plants or fibrous materials of any kind (Kinnear *et al.* in prep.). Analysis of these dietary items revealed that the gum contained no detectable nitrogen and that the fungi were deficient in the essential amino acid (EAA) lysine, but in addition, the EAA methionine was in excess. Hence, not only do we find that woylies are eating a lysine-deficient protein source, but also we find that the protein source has an amino acid imbalance. By known standards of mammalian nutrition woylies, as predicted, are eating unnutritious foods but are meeting their nutritional requirements as the result of microbial synthesis.

Competitive inadequacies of PGF mammals

In nature, niche theory predicts that we should observe mammals with PGF occupying niches that exclude other herbivorous mammals with different alimentary systems. But they also will be excluded from nutritional niches—in particular, those niches which provide nutritionally balanced foods. This does not mean that mammals with PGF will not thrive on nutritious diets for they will, but because of their trophic status, it means they will utilise such foods inefficiently relative to non-PGF competitors and thus they will be excluded from such niches.

There are, however, conceivable circumstances where dietary analyses may reveal that the foods eaten by some PGF mammals are balanced and nutritious. We have so far conceived of four situations:

(1) The food may be nutritionally complete, but contains toxic substances that are subject to microbial degradation.

(2) Nutritious foods are not limiting, i.e. a surplus exists.

(3) PGF mammals may occupy nutritionally complete niches during seasonal periods, i.e. the growing season.

(4) Competitors may be absent.

To illustrate the niche space of PGF mammals, both in the absence and presence of competitors, we have presented a series of figures representing the nutritional niche space for two dimensions only. In the absence of competition we observe simple niche expansion; in the presence of competitors, PGF animals are excluded from an area of the two-dimensional niche space (Fig. 1).

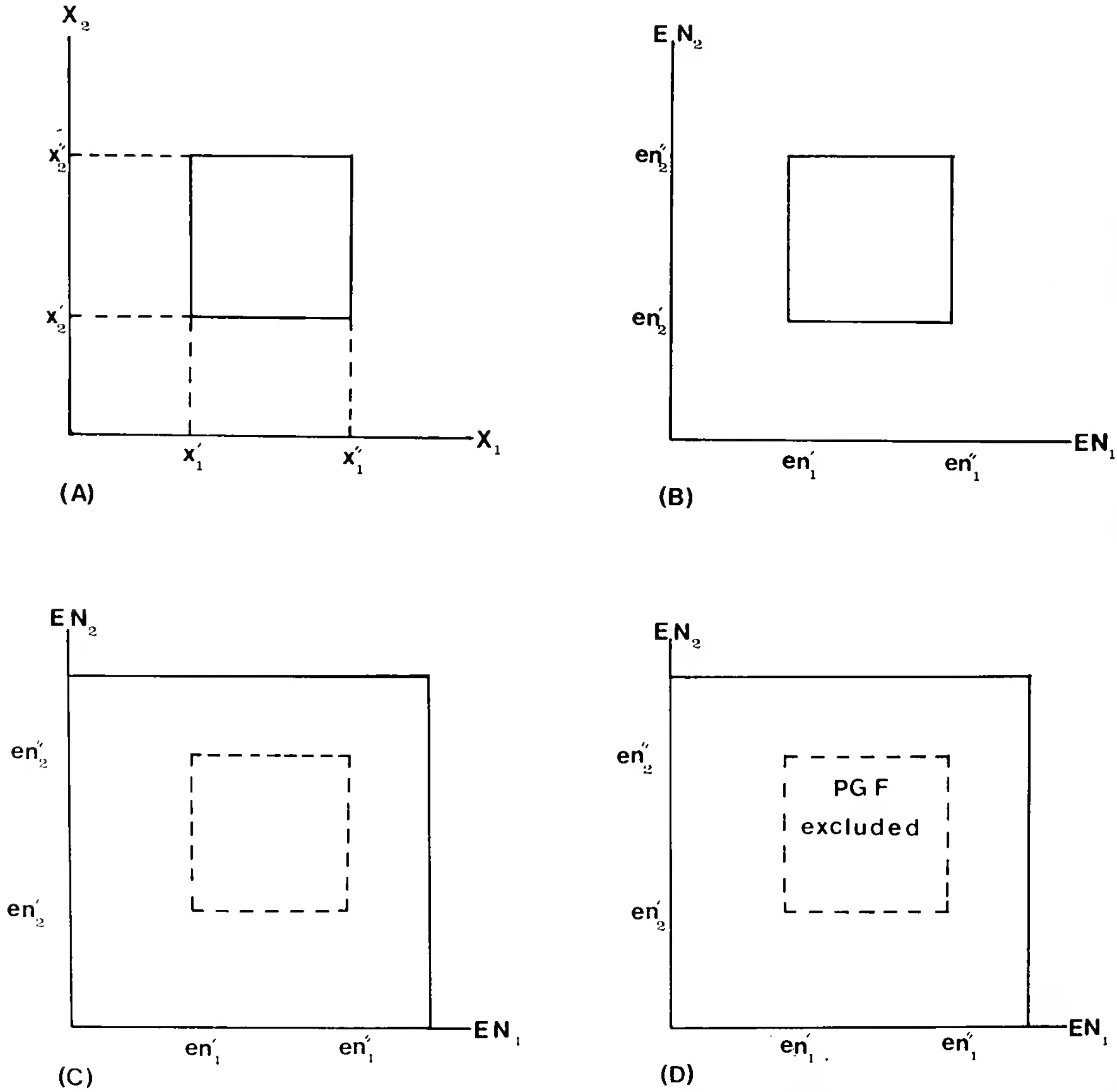

Figure 1.—The niche space restricted to two dimensions for the purpose of illustration (the concept is generalised to n-dimensions). A.—Hutchinson's fundamental niche: factors or variables affecting a given species are linearly ordered on a pair of rectangular axes and the limits $X''_1 — X'_1$ and $X''_2 — X'_2$ define an area (a 2-space) within which a species can survive and persist. B.—The fundamental nutritional niche: two essential nutrients are linearly ordered and the limits (en''_1, en'_1 etc.) denote an area within which a species survives and persists. C.—The nutritional niche space of a PGF species; the symbiotic interaction results in simple niche expansion in the absence of non-PGF competitors. The inner area represents the fundamental nutritional niche. D.—The nutritional niche space of PGF species under competition with non-PGF species. PGF species are excluded from regions of their fundamental niche space because they are competitively inferior.

Competitive interactions between PGF mammals

An immense number of feeding trials involving domestic ruminants has revealed that these animals possess an extremely versatile and adaptable alimentary system, for they have been fed an incredible array of foodstuffs—from newsprint to anchovies. These animals seem capable of eating almost anything, anywhere; their system of alimentation would seem to be the ultimate nutritional solution.

But such impressions are tempered when viewed from an ecological perspective, for ecological theory demands that co-existing species must avoid excessive niche overlap. We should therefore expect and observe niche partitioning of food resources by sympatric species of mammals with PGF. Furthermore, as a corollary, we should expect to observe specialisations in physiology and morphology.

Recent studies have borne out these ecological predictions. Hofmann (1973) has produced an impressive monograph on the African ruminants which describes, in great detail, the different morphological adaptations of the rumen which are correlated with dietary preferences. Hofmann has related stomach structure to the type of food eaten, and he has arranged a large number of African species into three major groups; (a) concentrate feeders—low fibre/succulent diets; (b) roughage feeders—fibrous diets; and (c) concentrate/roughage feeders—i.e. species that eat either foods depending on whatever is seasonally available.

Less information on nutritional-niche partitioning exists for the ruminant-like macropodids but from the available information a similar pattern is emerging. For example, the woylie rat-kangaroo stomach differs substantially from that of wallabies and kangaroos; moreover it is a concentrate feeder (as is the Tasmanian potoroo—Guiler 1971) which ensures that it does not overlap or compete with the three species of macropods using the same habitat (Kinnear *et al.* in prep.).

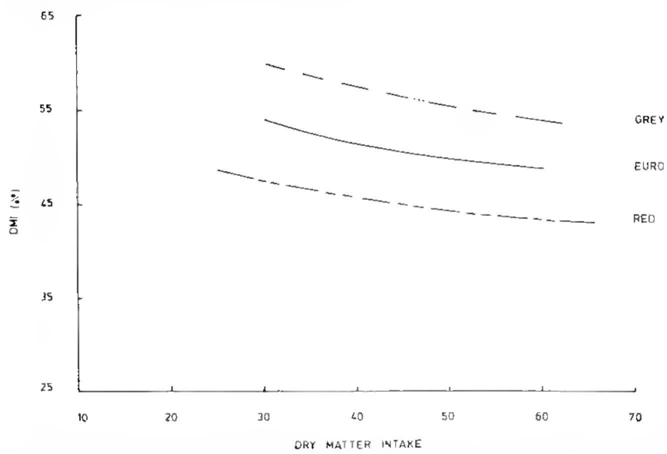

Figure 2.—The performance of 3 species of kangaroo in digesting fibrous diets. As dry matter intakes (dry matter wt. $kg^{0.75}$) increase, the percentage of dry matter digested (DMI (%)) tends to decline slightly for all species, but the significant points are the differences between the 3 species in extracting digestible energy from fibrous diets (after Prince 1976—with permission).

With respect to physiological adaptation and specialisation, differences between the three common species of kangaroos have been documented by Prince (1976). In comparative feeding trials, a standard diet containing fibre was fed to western grey kangaroos *(Macropus fulijinosus)*, red kangaroos *(Megaleia rufa)* and euros; appreciable differences in digestive efficiencies were noted.

The differences are illustrated in Figure 2 where it is evident that the three species differ significantly in their abilities to extract digestible energy from fibrous diets. The red kangaroo is least efficient in obtaining energy from fibre, which means that it must seek out nutritional niches that provide low-fibre foods; in the wild, they are known to do this (Newsome 1975). The opposite extreme is the grey kangaroo which is the most efficient, and Prince points out that the grey, which has a southern distribution, is more subject to cold stress (due to low temperatures and winter rains), and hence the ability to obtain more energy from fibre is an adaptive specialisation to the environment and probably necessary to assure reproductive success. Finally, the euro which is predominantly northern in its distribution (summer rainfall) must also contend with fibre but it can afford to be less efficient.

The prevailing view held by most animal scientists is that the rumen has evolved to cope with fibrous foods. But it is now clear that this view is untenable because PGF mammals eat a wide array of plant materials, many of which are low in fibre. Hofmann's study shows that the fibre-consuming ruminants are merely specialists and we also observe the same sort of specialisation in the case of macropods, i.e. the grey kangaroo and the euro.

Niche theory provides a more general explanation: the function and purpose of PGF is to allow these animals to occupy expanded nutritional niches. At this stage (apart from our woylie study) we cannot support this explanation by factual data because the need for such data has not been recognised, and hence it has not been systematically collected. We hope that this challenge will be taken up.

Discussion

There seems to be little reason to doubt that pregastric fermentation is indeed a flexible system of alimentation that has been moulded by the pressures of natural selection and competition. We observe a plethora of species (ca. 50 species of marsupials and > 200 eutherian) frequently existing sympatrically in closely-knit associations that seem to defy the competitivo exclusion principle. Mammals with PGF are the dominant vertebrate grazer/browsers throughout the world in contrast to the hindgut-fermenting mammals which are relict survivors of a previously dominant group (Moir 1965).

The climatic factors associated with the rise of PGF mammals are cold temperatures and aridity which do not favour continuous plant growth. This forced mammals to satisfy their complex nutritional requirements from vegeta-

tion that was either in a state of dormancy, senescent, or dead. The PGF mammals solved this nutritional challenge in a peculiar way—they largely abandoned herbivory by acquiring a decomposer trophic level which they housed in their forestomachs.

It is this microbial trophic level which imparts nutritional flexibility and which also enables nutritional specialisation. The key to the success of PGF mammals has been the near abandonment of herbivory in favour of linking their food chain to a captive-decomposer trophic level. A significant feature of this trophic level is its affinities with the soil-decomposer ecosystem (Hungate 1960), for such comparisons indicate that PGF mammals have domesticated anaerobic soil micro-organisms which have retained their ecological function—that of decomposing organic matter. When these relationships are recognised and appreciated, it is easy to understand why macropods of the arid zone can survive for extended periods while consuming drought-affected vegetation that is nutritionally equivalent to plant litter.

However, this nutritional theme of housing a microbial trophic level in the foregut is not without its shortcomings for there are competitive and energetic disadvantages. PGF mammals are inherently less efficient in converting and transforming food into animal biomass and, moreover, this inefficiency would seem to have reproductive consequences.

If one surveys the mammalian literature (e.g. Walker 1975) for data on fecundity, a pattern emerges: eutherian mammals with PGF usually bear 1-2 young and this is so regardless of size; macropodid marsupials are uniformly consistent in that they give birth to only one young at a time. Thus it would appear that mammals with PGF have difficulty in allocating their food resources to the production of young; this characteristic is in sharp contrast to the reproductive performance of some non-PGF herbivores, e.g. the rabbit and many rodents.

The macropodid marsupials are further handicapped energetically for reasons that they have a lower metabolic rate (MR) relative to most eutherians (Dawson and Hulbert 1969, Kinnear and Shield 1975). Dawson (1973) has advanced the view that marsupials are energetically primitive, but such views do not help to explain why so many eutherians find it advantageous to generate metabolic power and heat in excess of their homeothermic requirements.

Kinnear and Shield (1975) suggest some advantages: "A high metabolic rate enables rapid synthesis and storage of energy as well as accelerated neonatal development and growth during favourable periods. All of these would be advantages to an animal facing future energy stress." The authors cite as an example the MR of the white-tailed deer (*Odocoileus virginianus*) which is up to twice as high in summer than winter. This reduction in MR allows for a slower rate of utilisation of stored energy reserves which are rapidly accumulated during peaks of primary production during summer.

Metabolism is an adaptive physiological parameter which not only provides heat to maintain a mammal's body temperature but also determines an animal's biosynthetic potential, i.e. the rate at which it can create biomass. With this point in mind we can appreciate the shortcomings in combining the energetic inefficiencies associated with PGF with a marsupial rate of metabolism, and this would seem to have some relevance to the extinction of the giant macropodids. These species did not survive the climatic oscillations of wet and dry periods in the Quaternary which were superimposed on an overall trend of increasing aridity. The periods of primary production favouring reproduction and growth would have been too short for recruitment because these giant and metabolically sluggish marsupials would have lacked sufficient biosynthetic power to maintain a population. It is significant that the surviving macropodid descendants are smaller-sized species and, moreover, they are sexually dimorphic with the female being smaller and becoming sexually mature at an earlier age than the male.

Thus, in the case of extant kangaroos, each species has adults of two sizes, and when several species occur together as in the Goldfields region of Western Australia where the red, euro and grey are found, there are effectively adults of six size classes. The reason for the containment of these species within their ranges and realised niches requires further study, as Main (1978) has suggested for the western and eastern grey Kangaroos in south-eastern Australia. Should such studies reveal, as seems likely, that habitat specialisation and not inter-species competition is the regulating factor, then habitat specialisation and the nutritional niche of each species are much more highly developed than external morphology would suggest.

From the above reasoning on habitat and niche specialisation, it would seem to follow that habitat alteration and not competition caused past extinctions, and conversely the extant or successful species persisted because they can match their needs even when dietary resources are of poor quality, and so survive to reproduce.

We conclude our account on the following points: within the aerobic zones of the biosphere there are no empty nutritional niches, for all primary production on balance is utilised by consumers or decomposers. Extinction of faunas therefore does not necessarily create or open up nutritional niches, for such niches can be partitioned in a different manner until a new equilibrium is reached between consumers and decomposers. Nutritional niches disappear with the extinction of plant species and communities and, conversely, new niches arise when new plant communities evolve.

It is noteworthy that in arid and semi-arid Australia the one ungrazed habitat is acacia scrub extending from a sandy coastal situation inland to the mulga scrub. No marsupial survived to exploit this nutritional niche yet, this habitat with its tall acacia should have been within the range of the giant marsupials, many

of which are believed to have been browsers. Thus while the Australian fauna has many parallels with its eutherian counterparts, it is significant that the present fauna has no equivalents to the large African browsers, e.g. the Giraffidae. Apparently, the large macropod browsers were incapable of adapting to aridity by dwarfing as in other macropods (Main 1978), because smaller animals are undoubtedly denied the browse on trees and shrubs.

Elsewhere the eutherian browsers persisted in the face of increasing aridity, often by using water holes (Leuthold 1977), and it is significant that when such large species were released in Australia, e.g. the feral ungulates such as the camel, they have successfully colonised the acacia habitat.

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Vegetation mapping in Western Australia

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Abstract

Interest in conservation and wildlife management has increased the value of vegetation mapping as a form of resource inventory. Western Australia achieved an early lead in this field with the work of Diels (1906) and Jutson (1914) but thereafter initiative passed to the eastern States for a number of years until the establishment of a State-wide vegetation survey in Western Australia in 1964. The aims, objects and methods of this survey are described and its achievements in publication are listed.

Introduction

There are basically two different ways in which a field botanist can regard the plant cover of an area in which he is working. He can see it as composed of individual plant species, each to be named and classified, or he can see it in the mass as vegetation having properties of structure and life-form. The former is the taxonomist's viewpoint, the latter the biogeographer's. In the latter case the existence of species is always of interest but it is not the prime interest. Some biogeographers are interested in species as units of association studying their occurrence and relative abundance in different habitats, but others to whom the physiognomy of vegetation is the dominant interest may regard species as no more than incidental. Studies of vegetation are normally accompanied by mapping of vegetation units so that location and extent as well as physical characteristics may be documented, and as techniques of mapping have improved so has vegetation mapping grown as an art and a science.

A vegetation map may be defined as one which shows the nature of the earth's plant cover. Sometimes this cover is a natural one, unmodified by human action, as we still find today in the unsettled inland areas of the State, and sometimes it has been entirely created by man, as in intensive agricultural areas. In intermediate cases, for example, those parts of Western Australia that are under pastoral leases, there is a natural plant cover that has been or is being modified by man and his domestic animals. A vegetation map records what is there but in general crop mapping in agricultural areas is commonly regarded as a separate field, i.e. land-use mapping, while a vegetation map in the strict sense is expected to show natural plant cover as it exists or used to exist. In settled areas there is often an attempt to reconstruct a picture of the original or primaeval plant cover.

The data presented in vegetation maps may be interpreted in many ways and for many different purposes, including the following:—

Conservation: Vegetation mapping provides an inventory of plant communities and plant habitats, which is the basic information required for planning an adequate system of biological reserves. At a later stage a vegetation map of a flora and/or fauna reserve or national park is one of the basic necessities for planned management and control.

Environmental-impact studies. Facts about vegetation are a part of necessary basic knowledge when assessments of impact upon the environment made by proposed mining and other land development are being made.

Potential land use. A vegetation map is a useful basis for more detailed surveys of land potential for agriculture, pastoral use and forestry, and for soil and geological surveys. It shows height and density of vegetation and may be used as a "going" map for military purposes and for oil and mineral exploration.

Early work in Western Australia

Until quite recently the art of vegetation mapping had been very little practised anywhere in Australia. Difficulties in travel and communication, and lack of accurate topographic base maps were formidable obstacles. Gradually, however, as interest in conservation and wildlife management has grown, interest has grown also in vegetation mapping as a necessary form of resource inventory, and several mapping programmes have been set up, supported by the Interim Council for the Australian Biological Resources Study and by State Governments.

It is a common experience in mapping, whether it be topographic, geological or phytogeographic, that it begins with some rather imprecise sketch-maps usually at large scales made by the pioneers

and proceeds by successive revisions to greater precision at smaller scales. Before the introduction of aerial photography in the 1930s it was virtually impossible to map large areas accurately in detail and any precise vegetation mapping was confined to local studies. Larger areas had inevitably to be covered on a sketch-map basis and involved a large amount of guess-work. L. Diels for example furnished a coloured sketch-map at 1:27 000 000 of the whole continent as the end-papers to his book of 1906 but it cannot have been intended to give more than a general impression of the vegetation. Numerous other small-scale renderings of the vegetation of Australia appeared in atlases and geographies throughout the world, all of them unavoidably imprecise and unreliable.

It is interesting that in the early period Western Australia was well to the fore. Diel's book *Die Pflanzenwelt von West-Australien* (The plant world of Western Australia) published in German in 1906, which included the map mentioned above, was the only comprehensive and authoritative account of any Australian vegetation to be published prior to the first World War. Western Australia also produced the first State map of vegetation, when J. T. Jutson in 1914 produced a sketch map at 1:5 000 000 to accompany his classic work on physiography. The map was published in colour and distinguished nine basic vegetation types, alluding to two more (fringing forests and mangrove woodlands) in the legend. Acknowledgement was given to the Forests Department as the source of the information.

In 1928 the Forests Department reprinted the map with the addition of data contributed by C. A. Gardner on the distribution of the more important species of *Eucalyptus*. This map was again reprinted in 1967, without revision. In the meantime Gardner (1942) had published a general account of the vegetation of the State which included a small black and white map on a scale of 1:25 000 000 and this also was still based on Jutson.

Western Australia's early lead in this field was not maintained and the initiative passed in the 1920s to South Australia where the Botany Department of the University of Adelaide, the Waite Agricultural Research Institute, the CSIRO Division of Soils and the State Departments of Agriculture, Lands and Forests, between them mapped most of the south-eastern part of South Australia in terms of vegetation, or of soils and vegetation, at a considerable range of scales. This activity came to be known as the "Adelaide School" and was inspired by Prof. J. E. Wood of Adelaide who produced an integrated text and map in 1937. Important contributions were later made by Blake (1938) in Queensland and by Beadle (1948) in New South Wales, both of whom succeeded in mapping very extensive areas before aerial photography became available.

The introduction of aerial photography in the 1930s transformed the situation and it became possible to map vegetation accurately and rapidly. In Western Australia after World War II the Forests Department conducted detailed stock-mapping (1:63 360) of the State Forests in the south-west, and the pastoral section of the Department of Lands and Surveys produced a number of pastoral-classification plans at a scale of 1:250 000 in which the plant cover was mapped according to its estimated carrying capacity. Some other mapping was carried out by the CSIRO which conveyed vegetation information without mapping it directly. The CSIRO Division of Land Research published three surveys covering almost the whole of the Kimberley District in the north (Speck *et al.* 1960, 1964; Stewart *et al.* 1970) and another survey (Mabbutt *et al.* 1963) covered a strip typical of mulga country in the Murchison region.

These surveys were not vegetation surveys as such but mapped "land systems"; however, as vegetation is a component of a land system and detailed information was given in the explanatory text, it was possible to reinterpret for vegetation if desired. The same applies to the work of the CSIRO Division of Soils which has published three surveys in the south-west, covering the Margaret-Blackwood River area (Smith (1951), the Swan Coastal Plain (McArthur and Bettenay 1960), and the Merredin area (Bettenay and Hingston 1961). As close correlations were found between vegetation and soil types and notes on vegetation were given in the text, the soil maps could be similarly reinterpreted for vegetation.

A State-wide vegetation survey

Attempts to depict the vegetation of the whole of Australia accurately by drawing upon published sources had been made by Prescott (1931) and by Williams (1955) and these highlighted the serious lack of basic information from Western Australia which was shown to be by far the least known of any of the States. In 1964 it was resolved by Prof. M. J. Webb and the writer to promote a State-wide survey to redress the situation. This project which was called the Vegetation Survey of Western Australia has been carried on since, supported by the Department of Geography at the University of Western Australia where the cartographic work is done, and in the early stages by the King's Park Board, and latterly by the Interim Council for the Australian Biological Resources Study, both of which have provided finance for fieldwork and publication. Three maps have been contributed by the Western Australian Department of Agriculture (Smith 1972, 1973, 1974). Several previous accounts of the aims, objects and methods of the survey have been published (Beard 1966a, 1969, 1975a, Beard and Webb, 1974).

The first decision which has to be made on commencing such a programme is what scale is to be adopted, and here one has to consider the area involved, the man-power and finance available and the duration of the project. Obviously a survey of Lord Howe Island or even Tasmania can be made more intensive than one of Western Australia. It was decided that the 1:1 000 000 scale would be the most generally useful within the limits of feasibility. It has the advantage of being the same scale as the International Map of

the World topographic series, and as a French vegetation map series, the Carte Internationale du Tapis Végétal.

The question of scale is of fundamental importance. For the mapping of a given area, the larger the scale the larger the map and vice-versa. Alternatively, with a given size of map, the larger the scale the smaller the area the map portrays, and vice-versa. A vegetation map of the largest possible conceivable scale would be a diagram of a quadrat on which all the individual plants and their coverage were marked. Such a map inevitably represents a relatively tiny area. For the mapping of more extensive areas, the scale has to be reduced. It then becomes impossible to represent individual plants, and they have to be grouped into communities whose boundaries are mapped. At progressively smaller scales fewer communities can be represented and there has to be progressive generalisation of the map.

It therefore follows that for the vegetation mapper there can be no absolute concept of the plant community. The concept is dictated by the scale he is using and the ability to represent units on the map. To give concrete examples, the vegetation maps of Lord Howe Island (Pickard 1974) which covers 13 km^2, of Tasmania (Jackson 1965) covering 42 450 km^2, and of the Murchison Region of Western Australia (Beard 1976) about 385 000 km^2, represent units of quite a different order from one another, because of the progressive generalisation which is obligatory with increasing scale.

It follows also that there can never be any absolute standard for an inventory of plant communities of Australia since the number of communities is dependent upon the scale at which they are being considered.

Having made a general decision on the use of the 1:1 000 000 scale for principal publication, a special series of seven map sheets was designed in order to cover the State in the most economical manner (Fig. 1). The standard grid of the International Map of the World Series (also known in Australia as the Aeronautical Series) necessitates 14 sheets for Western Australia of which five straddle the eastern border and are only half within the State. The special series however is still built upon the standard grid of the smaller 1:250 000 series, shown as smaller rectangles in Figure 1. Basic mapping is done on aerial photomosaics at a scale of 1:63 360 rather than on individual aerial photographs because the latter would be too time-consuming. Adequate detail for the publication scale is obtained from the mosaics and is first reduced and drawn at 1:250 000, then reduced again and compiled at 1:1 000 000. The original 1:250 000 sheets are hand-drawn on film and are filed in the map library of the Department of Geography at the University of Western Australia. Dyeline prints can be obtained on request. Those of the 1:250 000 sheets covering the South-West Botanical Province where vegetation patterns show finer detail and where there is likely to be greater public interest, are being drawn on a standard topographic base and published as a separate series (Fig. 1.)

Classification and terminology

Having regard to the nature of this survey which was essentially a preliminary survey of a very large, little-known area, it was considered the most appropriate to approach the characterisation of vegetation on a physiognomic basis (Beard 1973c). Time would not permit the use of quantitative or phytosociological methods at this stage, however desirable they might be, and it was expected that they would be applied in later, more detailed, work. The broad principles of classification adopted in this survey, therefore, are those stated by Beard (1944, 1955). The basic unit is a floristic unit, the plant association. The association is the largest possible group with consistent plant dominants, either of the same or closely allied species. Associations may be divided into minor floristic groups and may be grouped floristically into alliances. Associations may also be grouped together, according to their physiognomy (structure and growth-form), into formations. The formation is thus a physiognomic unit.

Prior to 1964 the physiognomy, classification and nomenclature of Australian plant formations had been discussed by Beadle and Costin (1952) and by Williams (1955) but there was no generally agreed system. Many advantages seemed to be offered by the approach suggested by Küchler (1949) who drew up a number of simple life-form classes.

Küchler's system had the added advantage that it could be expressed as a mapping notation. It is not desirable that a map should depend entirely on its colours to distinguish units, as the eye may not readily differentiate between all of them, and in any case many of the maps have been published in black and white. The geologists employ a notation of this sort e.g. Tep= Tertiary, Eocene, Plantagenet Group, Ag=Archaean granite. Vegetation units can be simply numbered but this is rather a crude approach.

The trouble was that Küchler's system, while a brilliant idea, included illogical features and was framed to suit North American conditions. Dansereau (1951) reshaped the system into an elegant and logical classification capable of describing any vegetation community in the world. Unfortunately, the mapping notation became too unwieldy to put onto a map! A simpler system was therefore devised for practical use, which has come to be known as the Beard-Webb system (Beard and Webb 1974). It was felt that the notation should be of reasonable brevity and should convey the diagnostic features of the vegetation which are: 1, Nature and size of the dominant stratum and of other strata if of diagnostic importance; 2, Dominant or diagnostic plant species and 3, Density of the strata referred to in (1).

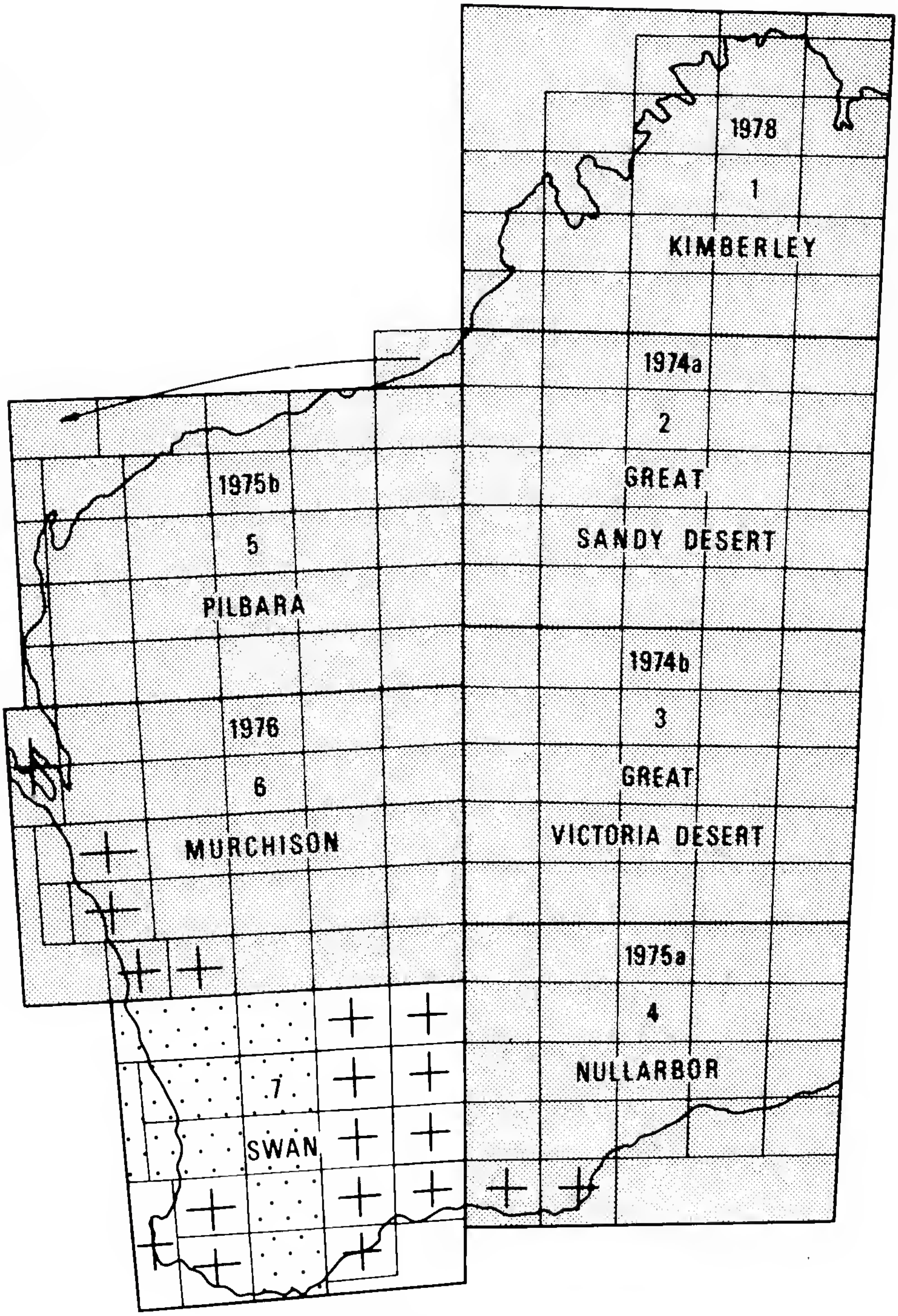

Figure 1.—Vegetation survey; progress in mapping and publication.

The Beard-Webb system is built up as follows:

(1) Physiognomy of dominant stratum (capital letters)—
- T Tall trees > 30 m tall.
- M Medium trees — 10-30 m tall.
- L Low trees < 10 m tall.
- S Shrubs > 1 m tall.
- Z Dwarf shrubs < 1 m tall.
- G Bunch grasses.
- H Hummock grass (spinifex).
- F Forbs.
- X Lichens and mosses.
- C Succulents.

(2) Floristic (lower case letters)—
- e Eucalyptus.
- a Acacia.
- t Triodia.
- x Heterogeneous (mixed or other).

(3) Density (lower case letters)—
- d Dense canopy. Projective foliage cover, > 70 per cent.
- c Mid-dense canopy. Projective foliage cover, 30-70 per cent.
- i Incomplete canopy, open not touching. Projective foliage cover, 10-30 per cent.
- r Rare but conspicuous. Projective foliage cover, < 10 per cent.
- b Barren, vegetation largely absent. Projective foliage cover negligible.
- p Scattered groups. No definite foliage cover.

The letter "C" has been introduced to the classification and defined as "succulents". Most of these are Chenopodiaceae, hence the letter "C", "S" being pre-occupied. In addition to the fully succulent samphires, this class is intended to include the semi-succulent saltbush and bluebush vegetation, which is locally very widespread in parts of the Australian Eremaea, as it is considered essential that these communities be recognized to have a unique character of their own, and differentiated from sclerophyll shrublands. The floristic component (e, a, t, etc.) can be differentiated as e_1, e_2 to indicate particular species, and other letters may be added as required, e.g. m. for Melaleuca.

The actual formulae are to be written with the floristic category first e.g. eMc, aLi: meaning respectively a eucalypt-dominated closed medium tree community (a eucalypt forest in fact) and an acacia-dominated woodland (mulga). The formulae are designed in this "triangular" form in order to be more readily comprehended at a glance. The central capital letter conveys the most important feature (physiognomy), the left-hand one floristics and the right-hand one density.

The principal, capital-lettered category is based upon Küchler's Group 1 Height, and is intended to accord mention primarily to the dominant stratum, e.g. eMc. If two or more strata are considered co-dominant, their symbols may be written together e.g. xSZc. Any diagnostically important strata may be included in this manner—eLr, aSr, pHi.

The floristic category serves to name the species or genera which are dominant or diagnostic, but as most West Australian communities are of simple composition or even single-dominant associations, this category will also to a large extent convey—from the known morphology of the species—a growth-form characteristic of the community. A category "heterogeneous" is provided for mixed communities in which no definite dominance asserts itself.

The third category, density, is the same as Küchler's Group II. Küchler's Group III is not directly included: the characters which it deals with will have been already incorporated in the formula if important i.e. if they are "salient features" otherwise they are disregarded. Dansereau has set up three other categories in his system: function, leaf shape and size, and leaf texture. All of these will be found to be conveyed by the floristic category and are therefore not separately required.

Specht's projective-foliage-cover classes have been introduced and related to the code letters, with the addition of a letter "d" for "Dense" not appearing in Küchler or in Beard (1969). It is intended in Australian work that "d" should apply to rain forests while "c" will be used for eucalypt forests which admit much more light even though tree crowns may be touching.

An attempt is being made to carry the treatment in the notation and terminology through into the map colour scheme. A colour spectrum ranging from blue for moist forest through to red for desert is in accord with general international practice and has been planned as follows:

- T Blue
- M Green
- L Orange
- S Yellow
- Z Grey
- G Olive
- H Red
- F Rare, not provided
- X Hachured
- C Brown

Density of the vegetation is conveyed by shade of colour, dark for dense, pale for open. The general transition from the desert southwards is expressed in the sequence of colours red-orange-yellow-green-blue, and northwards in red-yellow-olive-green. "Z" and "C" are mainly edaphically controlled and are therefore extraneous to the climatic sequence. Considerations of map design are involved at this stage and the colour sequences are designed to be aesthetically pleasing.

Table 1 shows the Beard-Webb classification with its associated nomenclature. It differs from the rather similar treatment of Specht (1970) in basing the classification upon the dominant stratum, not the tallest one, and is more in accord with ecological principles as well as being more suited to mapping. The second part of the table provides for wooded grass and shrub communities which have more than one significant layer. Grassland nomenclature follows Beard (1966b).

Table 1

Nomenclature of vegetation units as used in the vegetation survey of Western Australia

A. Communities with a single significant layer

Life Form/Height Class	Cover of dominant stratum				
	Dense d 70–100%	Mid-dense c 30–70%	Incomplete i 10–30%	Sparse r <10%	Very Sparse b Negligible
T Tall trees >30 m	Dense Tall Forest	Tall Forest	Tall Woodland	Open Tall Woodland	....
M Medium trees 10–30 m	Dense Forest	Forest	Woodland	Open Woodland	....
L Low trees <10 m	Dense Low Forest	Low Forest	Low Woodland	Open Low Woodland	Sparse Low Woodland
S Shrubs >1 m	Dense Thicket	Thicket	Scrub	Open Scrub	Sparse Scrub
Z Dwarf shrubs <1 m	Dense Heath	Heath	Dwarf Scrub	Open Dwarf Scrub	Sparse Dwarf Scrub
G Bunch Grasses	Dense Grassland	Mid-dense Grassland	Grassland	Open Grassland	Sparse Grassland
H Hummock grasses	....	....	Hummock grassland	Open Hummock grassland	Sparse Hummock Grassland
F Forbs	Dense Herbfield	Mid-dense Herbfield	Herbfield	Open Herbfield	Sparse Herbfield
X Lichens and mosses	....	....	Mat Plants	Open Mat Plants	Sparse Mat Plants
C Succulents	....	....	Succulent Steppe	Open Succulent Steppe	Sparse Succulent Steppe

B. Communities with more than one significant layer

Description	Cover of tree/shrub layer			
	Incomplete i 10–30%	Sparse r <10%	Very Sparse b Negligible	Absent
Wooded Bunch Grassland	Savanna Woodland	Tree Savanna .... Shrub Savanna	Sparse Tree Savanna Sparse Shrub Savanna	Grass Savanna
Wooded Hummock Grassland	Steppe Woodland	Tree Steppe .... Shrub Steppe	Sparse Tree Steppe .... Sparse Shrub Steppe	Grass Steppe
Wooded Succulent Steppe	Thickly Wooded Succulent Steppe	Lightly Wooded Succulent Steppe	Sparsely Wooded Succulent Steppe	Succulent Steppe
Heath with Trees	....	Tree heath	....	....
Heath with shrubs	....	Scrub heath	....	....
Heath with mallee	....	Mallee health	....	....

Progress of publication by the Vegetation Survey of Western Australia up to the time of writing (August 1978) is summarised in Figure 1. Five of the seven 1:1 000 000 map sheets have been published (Beard 1974, 1975b,c, 1976a, Beard and Webb 1974) and all but eight of the 1:250 000 map sheets are available (Beard 1969, 1972 a-e, 1973 a, b, 1976 b-f, Smith 1972, 1973, 1974). The survey is thus almost complete and has lifted Western Australia from the position of least to best documented of the States in terms of vegetation.

Future work

It is considered a desirable objective that coverage of Australia at the 1:1 000 000 scale should be completed as soon as possible. Tasmania was done in 1965 (Jackson 1965). State vegetation mapping projects have been commenced at the National Herbarium, Sydney, and at the Queensland Herbarium, but results have not yet been published. It is also a desirable objective that the mapping should be uniform. The authorities conducting geological surveys in Australia long ago decided to adopt uniform mapping standards for the general 1:250 000 series so that maps of any State are comparable. The questions of scale come up again here, however. The standards of the vegetation survey of Western Australia, the Beard-Webb classification system, the related map colours and so on, apply to the 1:1 000 000 and 1:250 000 scales for which they were devised. Uniformity at other scales is not suggested at this stage. Carnahan's (1976) map of Australia at 1:6 000 000, used a modified system based upon Beard-Webb, but changed to suit the requirements of his scale. More intensive, larger-scale, work would also have to set its own standards. This can already be seen happening in the work of B. G. Muir (1977) in the Western Australian Museum's "Biological Survey of the W.A. Wheatbelt", where the Beard-Webb system was expanded by the introduction of several new Life-Form-Height classes to provide for a more intensive definition of stratification. Thus Low Trees have been divided into two, LA 5 to 15 m tall, and LB

< 5 m; a class for the mallee life-form has been introduced and given the letter K, divided into both tree and shrub forms; shrubs are divided into five height classes, bunch grasses into two, while additional classes have been introduced for mat plants (M), herbaceous species (J), sedges (V) and cryptogams (X).

This development is regarded as both logical and welcome: it was always envisaged that something of this kind should and would take place when others came to hang more intensive work within the framework of the extensive survey. It serves to emphasise the point that scale dictates procedure.

Some other large-scale mapping has been carried out recently in Western Australia mainly for biological surveys and should be mentioned, e.g. Beard 1967, 1976g, McKenzie, Burbidge and Marchant 1973, Dames and Moore, 1975, Smith 1977. A small-scale map of the State at 1:10 000 000 has been prepared by reduction of the 1:1 000 000 sheets, recognising 25 basic vegetation units (Beard 1979a).

Derived benefits of the vegetation survey

Vegetation mapping was used for a study of palaeodrainage in the arid zone of the State, in which a map showing the approximate courses and directions of rivers which must have existed in more pluvial times was produced, Beard 1973d). The general accuracy of the interpretation has been confirmed by later work (van de Graaff *et al.* 1977).

Vegetation mapping has also been used to define phytogeographic natural regions in the State. Diels (1906) in treating Western Australia south of the tropic divided the area into two Botanical Provinces, the South-West Province and the Eremaean Province, and subdivided the former into 6 Botanical Districts, the latter (as far as known to him) into 2. Gardner (1942) added the concept of a Northern Botanical Province in the tropics. He later expanded Diel's Botanical Districts on a State-wide basis (Gardner and Bennetts 1956) so that there were now 5 districts in the Northern Province, 5 in the Eremaean, and 6 in the South-West. Burbidge (1960) incorporated the Botanical Provinces into Australia-wide Floristic Zones, and treated the Coolgardie Botanical District as an Interzone or ecotonal region lying between the Eremaean and South-West Provinces.

When vegetation mapping commenced it quickly became apparent that natural regionalisations were present in the grouping of vegetation units and were expressed by the map colours. To a very large degree these coincided with the intuitive ideas of Diels and Gardner and the mapping was therefore used as a means of laying down precise boundaries for the Botanical Provinces and Districts previously rather arbitrarily sketched on a small scale. The regional boundaries have been marked on the vegetation maps, and a new State-wide small-scale map has recently been produced (Beard 1979b).

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Plant physiologist amongst the grain legumes

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Abstract

This paper expresses a physiological approach to plant functioning based on studies of the efficiency of operation of plant organs and whole plants. Applied to nodulated legumes, it has the purpose of discovering how efficiently photosynthetic resources are utilized for nitrogen fixation and the synthesis of protein in vegetative parts and seeds. Comparisons between species suggest how differences in structure of organs and in growth habit and reproductive behaviour of the legume may influence its efficiency of functioning and yield of seed. The techniques illustrated for studying the economy of carbon and nitrogen might well be applied widely in studies of the productivity of non-leguminous crops.

Introduction

According to figures published by the Food and Agricultural Organization of the United Nations (FAO) the annual world yield of cereals and grain legumes amounts to approximately 1 500 million tonnes of harvested seed, the equivalent of three-quarters of the food dry matter used for human consumption. Although production of cereals within this total is more than ten times greater than that of legumes, the high protein content of legume seeds (Table 1), and the high levels of certain essential amino acids in their seed protein make legume grain uniquely important in the nutrition of man and his animals, especially when complementing a predominantly cereal diet (Siegel and Fawcett 1976).

Despite their importance to man most species of grain legumes have been subjected to much less extensive research than have cereals and other major crop plants. This becomes apparent when examining the volume of literature generated annually on different crops, the extent of national and international funding for research on leguminous versus non-leguminous crops, and the deployment of scientific personnel within research institutes concerned with the breeding and physiology of agriculturally-important plants.

The sad state of grain legumes on the world scene is also obvious when one follows changes in their productivity over the past twenty years, as indicated by yield figures given by the FAO. During this period average yields of cereal crops per hectare have risen by some 65%, due especially to the development of high-yielding cultivars of rice, wheat and maize, but little or no improvement is evident over the same period in productivity of most of the major grain legumes. Even in those species subjected to intensive selection programmes, for example soybean (*Glycine max* (L) Merr.) and garden pea (*Pisum sativum* L.) the improvement in yield per hectare over the 20-year period has been modest—of the order of 20-35%. This situation, combined with the low baseline productivity of legume crops as a whole (Table 1), the uncertainty of yield realization from one season or soil type to the next, and the notorious susceptibility of grain legumes to diseases, pests and environmental stress, would make one doubt whether further increases in funds and manpower should be devoted to their exploitation as crop plants.

Despite this distressing situation much can still be marshalled in defence of grain legumes. Firstly, it may be argued that their usefulness and productiveness should be assessed primarily in terms of protein yield. When viewed on this basis the comparisons with cereal crops become much more favourable, with several legume species outyielding cereals in protein per hectare by a considerable margin (Table 1). Moreover, in the case of peanut (*Arachis hypogaea* L.) and soybean a second valuable product, oil, is present in large amount in the seed. Secondly, the role of legumes in crop rotations should be recognized. In many parts of Asia, for example, grain legume crops are often grown at times of the year not suitable for cereals and under climatic conditions inferior to those allotted to the cereal. Lower yields from the legume are to be expected under these conditions, but, the fact that a second, nutritionally-valuable crop can be included in the year's cultivation, commends use of the legume. Thirdly, many grain legumes are short-cycle crops, occupying the ground for a much shorter period of time than in the case of many cereal crops; again comparisons based on yield of seed per hectare are unfair. Finally,

Table 1

World production and average yields of major grain legumes and cereals

Grain legumes	Production 1974 (million tonnes/yr)	Average yield 1965–74 kg/ha	Protein level in dry weight of seed %	Average seed protein yield 1965–74 kg/ha	Major producing countries (in order of importance as producers) 1974*
Soybean (*Glycine max* (L.)Merr.)	56·8	1 295	38·5	499	USA, China, Brazil, Indonesia, Mexico, USSR, Canada
Peanut (in shell) (*Arachis hypogaea* L.)	17·6	879	28·6	251	India, China, Nigeria, Senegal, Sudan, Burma, USA
Dry beans (*Phaseolus* spp.)	11·5	484	26·0	126	Brazil, India, China, Africa, USA, Mexico, Europe
Dry pea (*Pisum sativum* L.)	11·7	1 117	23·0	257	*USSR*,† China, W. Europe, USA, Ethiopia, S. America
Chickpea (*Cicer arietinum* L.)	5·9	617	19·9	123	*India*, Pakistan, Mexico, Ethiopia, Turkey, Burma
Broad bean (*Vicia faba* L.)	5·2	1 076	27·5	296	*China*, Italy, Egypt, U.K., Morocco, Ethiopia, Brazil
Vetches (*Vicia* spp. *Lathyrus* spp.)	2·1	1 241	27·5	341	*USSR*, Turkey, Spain, Poland, Morocco, Greece
Pigeon pea (*Cajanus cajan* (L.) Millsp.)	1·5	653	22·1	144	*India*, Africa, Latin America
Cowpea (*Vigna unguiculata* (L.) Walp.)	1·1	330	26·4	87	*Nigeria*, Upper Volta, Uganda, Asia, USA
Lentil (*Lens esculenta* Moench.)	1·2	609	24·5	149	India, Turkey, Ethiopia, Syria, USSR, W. Europe
Lupin (*Lupinus* spp.)	0·8	828	34·5	286	*USSR*, Poland, Australia, W. Europe
Others	3·3	522	....	....	
Total legumes	118·7	....	....	....	
Total cereals‡	1·357	1 750	11	193	

* Calculated from average values for seed protein content given in the Table.
† Where the name of a country is printed in italics its contribution accounts for more than half of the world's production.
‡ Includes wheat, barley, maize, sorghum and rice.

the unique contribution made by legume crops to soil fertility through their nitrogen-fixing symbiosis with *Rhizobium*, must be recognized. According to data provided by Nutman (1976) this can amount to 60-210 kg N per hectare per growing season. The attendant savings in reduced input of synthetic nitrogen fertilizers are likely to be quite substantial, whether in terms of expense to the farmer, or, indirectly, as a reduction in run-off of nitrogenous fertilizer residues into surrounding ecosystems.

The challenge then to students of the grain legumes is to assess from a variety of viewpoints the future value of these plants on the world agricultural scene. Agronomists will contribute by indicating how better management practices can lead to higher seed yield under a range of soil types and environments. Plant breeders will contribute by developing high-yielding cultivars resistant to disease, adapted to specific environments, and productive of better quality protein. The research of plant physiologists is likely to provide a fundamental understanding of how legumes function and an indication of the processes likely to limit production of seed protein under a range of agricultural conditions.

Questions relating to the productivity of plants require detailed knowledge of the integrated functioning of the whole plant and its parts and investigations of the vast spectrum of related events and processes at structural, physiological and biochemical levels which accompany development of the plant and its organs during growth. The purpose of this paper is to highlight this type of approach as applied to grain legumes, concentrating particularly on studies conducted by the author and his colleagues in Belfast, Northern Ireland and currently at the University of Western Australia. The first section of the paper deals with investigations of the functioning of nodulated roots, especially in relation to their utilization of carbohydrate for nitrogen fixation. The second section concerns the developing legume fruit and the mechanisms involved in its conversion of imported assimilates into the reserves of seeds. The third section is an examination of the functioning of the whole grain legume, in an attempt to visualize how it deploys its photosynthetic product for vegetative growth, nitrogen-fixation, and the storage of protein in seeds.

The functioning of nodulated roots

The primary function of plant roots is to supply minerals, water, and certain synthetic products to the shoot system. In legumes the synthetic functions of below-ground parts assume unusual importance, due to the nitrogen-fixing activities of nodules or the assimilation in roots of combined forms of nitrogen such as ammonium or nitrate (Pate and Wallace 1964; Wallace and Pate 1965; Oghoghorie and Pate 1971).

It is now generally agreed that ammonia is the first stable product formed during nitrogen fixation by the bacteroids of the nodule (Bergersen 1971; Dilworth 1974), and that its assimilation into organic compounds probably takes place via the glutamate synthase/glutamine synthetase system of the host cytoplasm of the bacterial tissue (Miflin and Lea 1977). From the glutamine produced by this system, other secondary products form, these and glutamine being exported from the nodule to the plant shoot through the transpiration stream (Pate 1971).

Decapitated roots and detached nodules of grain legumes commonly bleed a fluid from their xylem, and this can be readily collected and analysed to reveal which compounds are being utilized for export of fixed nitrogen. Some grain legumes (e.g. *Lupinus* spp., *Pisum* spp. and *Vicia* spp.) export upwards of 70% of their fixed nitrogen as the amides glutamine and asparagine, the latter compound usually predominating (Pate *et al.* 1969; Gunning *et al.* 1974), whilst in other legumes (e.g. *Phaseolus* spp., *Vigna unguiculata* (L.) Walp.) the ureides allantoin and allantoic acid are the principal exports (Atkins *et al.* 1978). These various nitrogenous products are readily labelled with ^{14}C and ^{51}N following feeding of the legume shoot with $^{14}CO_2$ and its root gas space with $^{15}N_2$ (Pate 1962; Oghoghorie and Pate 1972; Herridge *et al.* 1978), indicating that the compounds in question are true metabolic products of the fixation process.

Roots are of course dependent on carbohydrates received from the shoot as translocated sugar. Some of this carbohydrate is consumed in respiration of the nodulated root, some is used in formation of dry matter during growth of roots and nodules, and some serves as carbon source for formation of the fixation products which ultimately leave the root in the transpiration stream. The extent of these different forms of usage of carbonhydrate has been assessed during growth of two legumes, white lupin (*Lupinus albus* L.) (Pate and Herridge 1978) and cowpea *(Vigna unguiculata)* (Herridge and Pate 1977). Carbon incorporated during growth is assessed by measurements of dry weight gains of root and nodules over specific intervals of growth. The respiratory output of the enclosed nodulated root of the intact plant is measured continuously by a gas-flow system involving collection of respired CO_2 in Pettenkoffer assemblies (Minchin and Pate 1973), and the proportion of this CO_2 efflux due to nodules is estimated by comparing the specific activity of respiration of freshly detached nodules with that of their supporting root. Finally, the types and concentrations of compounds in xylem exudate of the nodulated root are assessed, and, by relating the C:N ratio of these exports to the total nitrogen increment of the shoot, the amount of carbon cycled through the root as fixation products is estimated.

In both cowpea and white lupin the carbon used in export of fixed nitrogen comprises the largest item of the carbon budget of the nodule, respiratory losses from the nodule the next largest item, and the incorporation of carbon into nodule dry matter the least expensive item. The carbon balance of the whole nodulated roots shows root respiration to be the largest consumer of carbohydrate. The large tap root of lupin is clearly more expensive to maintain than the less extensive root system of the cowpea. When their consumption is compared in relation to how much nitrogen they fix, nodules of lupin are found to use carbon less efficiently than those of cowpea (Table 2; Fig. 1). One reason for this is the higher C:N ratio of the amides exported from lupin nodules than of the ureides exported from cowpea nodules, but CO_2 efflux per unit of nitrogen fixed is also greater from nodules of lupin than of cowpea (Table 2), suggesting that other elements are involved in efficiency of operation.

Table 2.

*Economy of carbon in nitrogen-fixing nodules of two grain legumes.**

Species	*Vigna unguiculata*	*Lupinus albus*
	days	
Period of growth	0.78†	0.94†
	mg.plant^{-1}	
N fixed	726	788
N exported	705	761
C used in export of N.‡	969	1 789
C lost as CO_2 in nodule respiration	789	1 372
C incorporated into nodule mass	253	298
Total C requirement of nodule	2 011	3 459
	g atom . g atom^{-1}	
Total C required/N fixed	3.23	5.12
C exported/N exported	1.60	2.74
C respired/N fixed	1.27	2.02

* Data from Herridge and Pate 1977; Pate and Herridge 1977; Atkins, Herridge and Pate 1978.

† Vegetative growth and early fruiting.

‡ Estimated from the amount of N exported and the C:N ratio of xylem sap.

Since nodules have a relatively high rate of consumption of translocate in proportion to their mass, their functioning in nitrogen fixation is especially vulnerable to a decline or interruption in supply of photosynthate from the shoot. How-

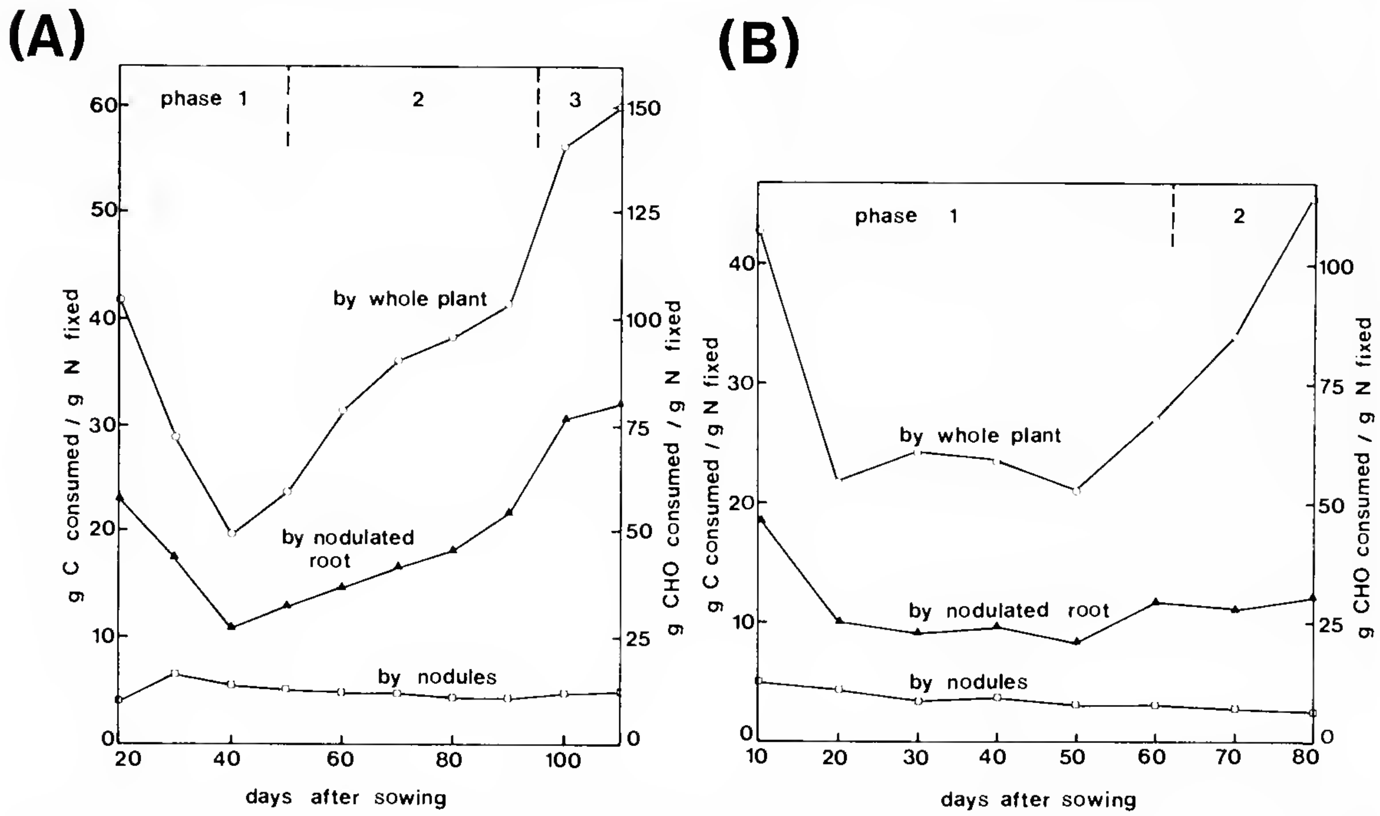

Figure 1.—The cost in terms of carbon consumption (as net photosynthate) of nitrogen fixation by nodules, nodulated root or whole plant over the life cycles of two grain legumes. (A) *Lupinus albus* L. (cv Neutra), and (B) *Vigna unguiculata* (L.) Walp. (cv Caloona). Phase 1 refers to vegetative growth before flowering, Phase 2 to flowering and early fruiting, Phase 3 to the final stages of fruiting. Data of (A) from Pate and Herridge 1978, and of (B) from Herridge and Pate 1977.

ever, they appear to possess a strategy of diurnal functioning in which sugar and polysaccharide built up during the day serve as carbon sources for fixation at night, thus allowing the nodule to fix much more nitrogen at night than would be possible were it to have to rely solely on current translocate (Minchin and Pate 1974). In garden pea (*Pisum sativum* L.) and cowpea, removal of the shoot causes within 24-48 hours a marked decline in the nitrogen-fixing activity of the root, as gauged by acetylene-reducing performance (Halliday 1976), but in broad bean (*Vicia faba* L.) or white lupin, fixation continues unabated for several days after removal of the shoot, suggesting that carbohydrate reserves of the tap-root might be made available as a substrate for nitrogen fixation. Drought-induced defoliation can also cause root reserves to be utilized for nitrogen fixation (unpublished data).

It has recently proved possible to compare experimentally-obtained values for CO_2 efflux of nodules with theoretical estimates of the costs, in terms of respired CO_2, of providing the ATP and reductant necessary for converting N_2 to NH_3, and for assimilating this ammonia into the compounds known to be exported from the nodule (Atkins *et al.* 1978). A summary of the relevant calculations (Table 3) shows that, for the three grain legumes studied, estimates of CO_2 output based on the theoretical reouirements for ATP by the nitrogenase system and ammonia assimilating reactions exceed by a substantial margin the experimentally-observed CO_2 output of the nodules. The differences involved appear to be greater in one legume (cowpea) than in the other two (garden pea and white lupin). The discrepancy between observed and predicted CO_2 efflux would be partly resolved were the nodule to economise in its carbon usage by refixing some of its respired CO_2, and to utilize this carbon in synthesis of the carbon skeletons of the compounds employed in transporting fixed N to the shoot. The demonstration of an active phosphoenol-pyruvate carboxylase system in nodules of *Lupinus angustifolius* L. by Christeller *et al.* (1977) suggests that nodules assimilate CO_2, and do so at a sufficiently fast rate (up to 0.8 molecules of CO_2 incorporated per atom of N fixed) to effect a considerable saving in terms of imported carbon from the shoot. It remains to be seen whether this applies to legumes generally.

The most likely source of discrepancy between observed and predicted values for CO_2 output from N-fixing nodules relates to the uncertainty of the in vivo requirements of the nitrogenase for ATP. The estimates of Table 3 assume that 4 ATP molecules are needed per electron pair utilized by nitrogenase, a value regarded as an average estimate for the performance of isolated nitrogenase in vitro (Dilworth 1974). In living bacterial tissue nitrogenase might operate at much lower cost since the structural configuration of the enzyme system in vivo might not require the continuous stabilization involving ATP hydrolysis needed to maintain activity of the extracted enzyme (Atkins *et al.* 1978).

Table 3.

Theoretical estimates of and experimental observations on CO_2 production by nitrogen-fixing nodules of three grain legumes.

	Vigna	*Lupinus*	*Pisum*
(A) Theoretical Estimates (1)			
	mol ATP . mol NH_3^{-1}		
1. ATP requirements for synthesis of organic solutes of nitrogen from NH_3 (2)—			
amino acids	0.40	0.84	0.48
glutamine-amino	0.20	0.24	0.30
glutamine-amido	0.05	0.06	0.08
asparagine-amino	0.20	1.34	1.26
asparagine-amido	0.15	1.01	0.95
ureide	2.10	—	0.30
Total cost for NH_3 assimilation	3.10	3.49	3.37
2. CO_2 output associated with nitrogen assimilation (3)	mol CO_2 . mol NH_3^{-1}		
N_2 reduction to NH_3	1.75	1.75	1.75
NH_3 incorporation into organic N solutes	0.52	0.58	0.56
Total N assimilation cost	2.27	2.33	2.31
3. CO_2 output for growth and maintenance.	mol CO_2 . mol NH_3^{-1}		
C loss as CO_2 in nodule formation (4)	0.06	0.06	0.11
C loss as CO_2 in nodule maintenance (5)	0.05	0.06	0.01
Total nodule cost	0.11	0.12	0.12
4. Total CO_2 output.	mol CO_2 . mol NH_3^{-1}		
Items 2 and 3	2.38	2.45	2.43
(B) Experimental Observations.			
	mol CO_2 . mol NH_3^{-1}		
Output of respired CO_2 from nodule	1.27	2.02	1.73

(1) As detailed by Atkins *et al.* (1978).

(2) Synthetic pathways as described by Atkins *et al.* (1978), proportions of amino compounds produced as suggested from xylem sap analysis.

(3) Calculated as 6 ATP per CO_2, assuming that the P/2e- ratio of oxidative phosphorylation is 3.

(4) Calculated using 0.2 g CO_2 produced . g dry wt^{-1} synthesized (Penning de vries *et al.* 1974).

(5) Calculated using 30 mg glucose . g dry matter $^{-1}$ day^{-1} (from Penning de Vries 1975).

(6) From studies of Minchin and Pate 1973 *(Pisum)*; Herridge and Pate 1977 (*Vigna*); Pate and Herridge 1978 (*Lupinus*).

An important factor in the efficiency of functioning of nitrogenase relates to its activity in converting protons to hydrogen gas, a process which will compete for electrons with the reduction of nitrogen gas to ammonia (Dixon 1975). In nodules formed by certain legume-*Rhizobium* associations hydrogen evolution is high relative to ammonia formation; in others a hydrogenase system re-utilizes much of the hydrogen which is produced, the attendant conversion to water generating significant amounts of ATP (Dixon 1975; Schubert and Evans 1976). It follows that nodules possessing an active hydrogenase system will have a lower requirement for ATP than those not so endowed, and that their overall consumption of carbon in nitrogen fixation will be correspondingly reduced. It appears that the strain of *Rhizobium,* not the host plant, is responsible for determining the level of hydrogenase in the nodules of a particular association (Schubert *et al.* 1977) but that ontogenetic and environmental factors may modify H_2 evolution from nodules during the growth cycle of a specific association (Bethlenfalvay and Phillips 1977). This suggests that nodules may not operate at a constant level of hydrogenase activity relative to nitrogen fixation. There is still considerable confusion surrounding the significance of hydrogen evolution and hydrogenase activity in nodule functioning, but it would be especially interesting to see whether the apparent differences in efficiencies of carbon usage by the N-fixing associations in Table 2 relate to effects of this nature.

The structure and functioning of fruits

Grain legumes display great variation in size, shape and structure of their fruits. In some (e.g. peanut *(Arachis hypogaea)* and bambarra ground nut *(Voandzeia subterranea* Thon.)) the fruits develop underground and lack chlorophyll. In most, however, the fruits are green and are borne aerially, often in a well-illuminated situation in the canopy. They thus have the potential for photosynthesis and for attracting water and nutrients from the parent plant through their transpirational activity.

The legume fruit consists of a single carpel containing 1-10 or more seeds. Its vascular network comprises a ventral longitudinal strand, two dorsal longitudinal strands supplying the seeds, and a network of veins traversing the lateral walls of the pod and connecting above and below with the longitudinal strands. A gas cavity of variable size and shape forms within the carpel as the young fruits develop. During later growth this gas space is encroached upon by the developing seeds (Harvey *et al.* 1976; Flinn *et al.* 1977).

Anatomists recognise three basic layers in the pod wall of legumes—exocarp, mesocarp and endocarp (see Esau 1965; Fahn 1974; Fig. 2). The exocarp comprises a heavily-cutinized epidermis, poorly supplied with stomata, and, in some genera, an underlying hypodermis of lignified cells. The mesocarp consists of 5-40 layers of thin-walled, highly vacuolated cells, usually well supplied with plastids. The outer mesocarp contains the bulk of the chlorophyll and displays prominent air-spaces, especially adjacent to stomata (Fig. 2). The inner mesocarp shows few, if any, air spaces and contains the vasculature of the pod wall. The endocarp consists of one or more layers of sclerenchyma, an inner epidermis, and, in some genera, an intervening zone of parenchyma. Since cultivated legumes have been selected for non-shattering pods the fibrous component of the endocarp is usually much reduced in comparison with ancestral forms of the species (Zimmermann 1936). In certain grain legumes, for example the "mange tout" forms of garden pea, sclerenchyma may be completely absent, making the fruits soft and edible.

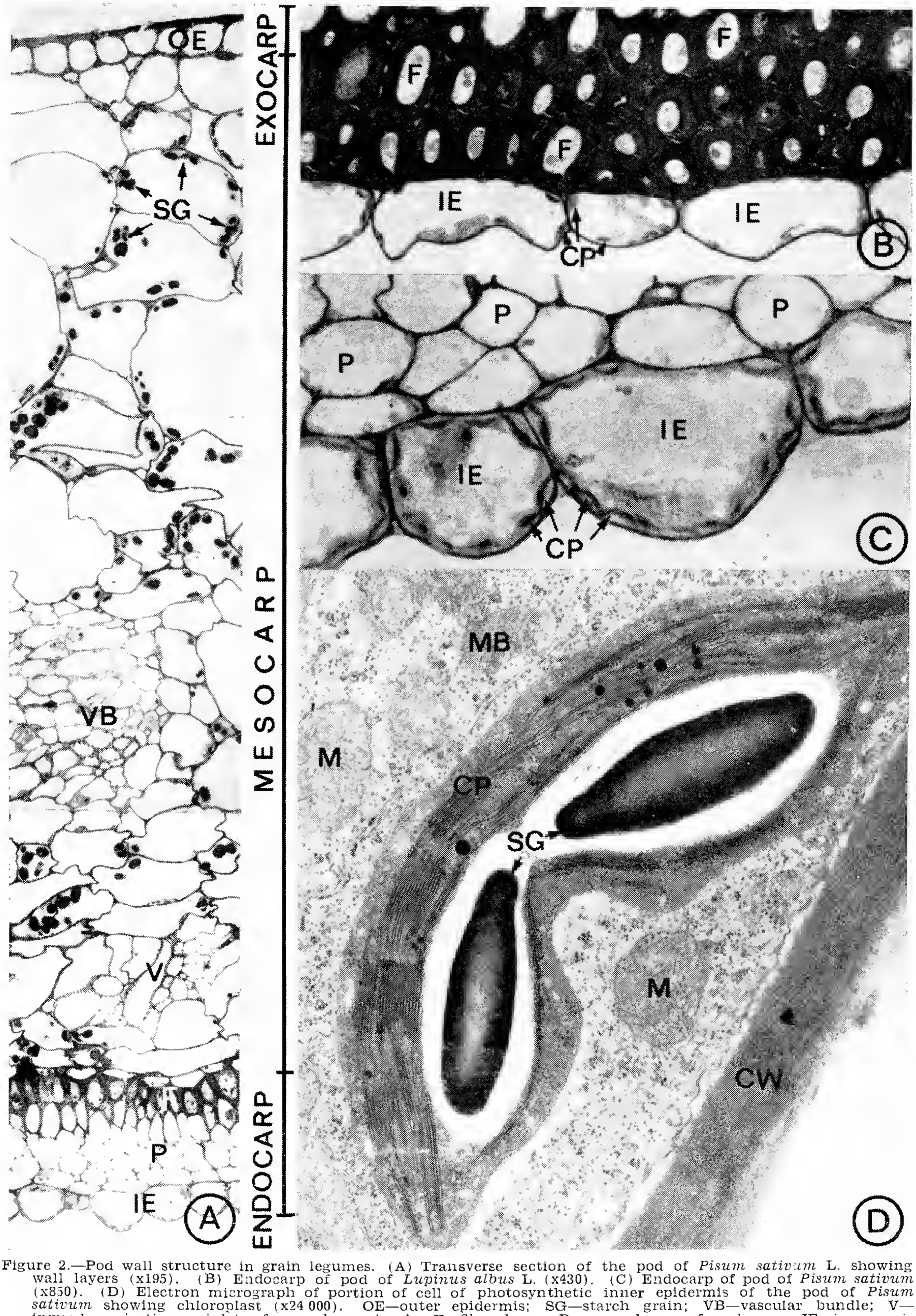

Figure 2.—Pod wall structure in grain legumes. (A) Transverse section of the pod of *Pisum sativum* L. showing wall layers (x195). (B) Endocarp of pod of *Lupinus albus* L. (x430). (C) Endocarp of pod of *Pisum sativum* (x850). (D) Electron micrograph of portion of cell of photosynthetic inner epidermis of the pod of *Pisum sativum* showing chloroplast (x24 000). OE—outer epidermis; SG—starch grain; VB—vascular bundle; V—inward projecting veinlet of vascular network; F—fibre layer; P—parenchyma of endocarp; IE—inner epidermis (photosynthetic); CP—chloroplasts of inner epidermis; M—mitochondria; MB—microbody; CW—cell wall. (Photographs kindly supplied by Dr. J. Kuo, Botany Department, University of Western Australia).

The pod walls of grain legumes are far from opaque, with up to half of the photosynthetically-active radiation received at the pod surface being transmitted to the inner epidermis (Atkins *et al.* 1977). In many genera (e.g. *Lupinus, Pisum, Vigna, Glycine, Cajanus, Cicer*) the cells of the inner epidermis are equipped with chloroplasts (Kuo and Pate unpublished; Fig. 2) and in some cases (e.g. *Pisum sativum* and *Lupinus albus*) the free-ending veinlets of the vasculature of the pod wall project inwards from the main vasculature to terminate almost at the surface of the endocarp, an adaptation, one might suppose, for collection of assimilates produced by the photosynthetic endocarp. In *Lupinus albus* these veinlets consist solely of phloem (Kuo and Pate unpublished) a feature consistent with a retrieval function within the pod wall.

Several physiological studies on grain legume fruits have provided information directly relevant to pod structure. Rates of exchange of CO_2 and transpiration rates are low, in comparison with leaves, as suggested by the structural features of the outer epidermis of the pod (Flinn and Pate 1970; Crookston *et al.* 1974; Andrews and Svec 1975). Poor ventilation also results in high concentrations of CO_2 (0.05-2.5% by volume of the fruit's gas space) (Harvey *et al.* 1976; Atkins and Pate 1977), much of this CO_2 being attributed to respiration of the developing seeds. Since CO_2 levels in the gas space are lower in illuminated than in darkened fruits, photosynthetic recycling of carbon by the internal tissues of the fruit is suspected. In *Pisum sativum*, a species with chloroplasts in its inner epidermis, injection of $^{14}CO_2$ into the gas cavity of an illuminated fruit leads to labelling of the pod but not the seeds, but neither pod nor seeds become labelled if the $^{14}CO_2$ injected into a fruit in darkness (Flinn *et al.* 1977). Labelled assimilates formed from $^{14}CO_2$ injected into an illuminated fruit can be traced first to the vascular network of the pod and then to the seeds, confirming the pod's role in recycling respired carbon back to the seeds.

Up to 25% of the chlorophyll of the pod of garden pea is contained in the inner epidermis, and this single layer also contains significant fractions of the pod's CO_2-assimilating enzymes, ribulose diphosphate carboxylase and phosphoenolpyruvate carboxylase (Atkins *et al* 1977). The last of these two enzymes may function particularly well in the CO_2-rich environment of the endocarp, and it is significant that the same enzyme occurs in high concentration in seeds of certain grain legumes (Hedley *et al.* 1975; Atkins and Flinn unpublished data).

Using data for compositional changes in pod and seed during growth, information on the day by day exchange of CO_2 and transpiration of the fruit, and analysis of the xylem and phloem fluids supplying the fruit with water and assimilates, it has proved possible to construct a quantitative model of a legume fruit's functioning based on its intake of carbon, nitrogen and water through xylem and phloem. The model for white lupin, as described by Pate *et al.* (1977) (see Fig. 3), indicates that 98% of the imported

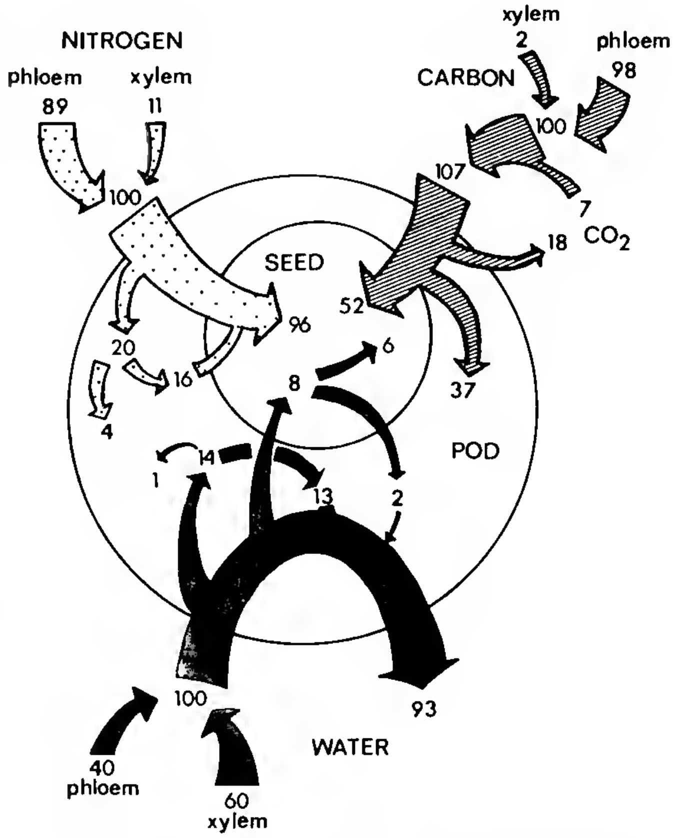

Figure 3.—Economy of carbon, nitrogen and water in a fruit of lupin (*Lupinus alba* L. cv Neutra). Deliveries through xylem and phloem are expressed relative to a net intake of 100 units of a specific commodity. Net photosynthesis, respiration loss, transpiration, water losses from tissues during fruit ripening and nitrogen mobilization from pod to seed are depicted. The weight ratio of imports over the life of the fruit is C : N : H_2O :: 12 : 1 : 600. (from Pate *et al.* 1977; Sharkey 1977).

carbon, 89% of the nitrogen and 40% of the water enters through phloem, the remainder through xylem. A fully-illuminated fruit effects net gains of carbon during the photo-periods of all but the last two weeks of its life (Sharkey 1977), but in no week of its life do the net daily gains of CO_2 from the outside atmosphere compensate for the night time loss of CO_2 from the fruit. Net respiratory losses increase dramatically as the fruit ages, due to increasing CO_2 output from the seeds and loss of chlorophyll and of photosynthetic performance by the pod.

Of every 100 units of carbon imported by a white lupin fruit over its life, 52 are eventually incorporated into seeds, 37 into non-mobilizable materials of the pod, and the remaining 11 lost as a net efflux of CO_2 to the outside atmosphere. By contrast 96% of the nitrogen entering the fruit ends up in the seeds, this element being mobilised to the seeds from temporary storage in the pod with 80% efficiency (Fig. 3).

The heavy dependence of legume fruits on phloem-borne assimilates and their low attraction of xylem-mobile solutes through transpiration, results in fruits, and especially seeds, having a final composition closely resembling that of phloem translocate (Pate *et al.* 1977; Hocking and

Pate 1977). In particular they exhibit low levels of elements only sparingly mobile in phloem (e.g. Ca and Mn), and under conditions of shortage of these elements seeds are likely to be the first to show deficiency symptoms. This is well displayed for manganese deficiency in the "marsh spot" disorder of peas (Reynolds 1955) and for the split-seed syndrome associated with deficiency of the same element in lupins (Perry and Gartrell 1976; Hocking *et al.* 1977). Similarly a reduction in transpiration of a fruit by enclosure can cause deficiency symptoms of calcium to occur in fruits, suggesting how critically important the transpirational attraction of xylem-mobile nutrients is in the normal development of the fruit (see Wiersum 1966). In underground fruits of legumes such as peanut the supply of Ca through the fruit stalk is supplemented by absorption of the element by the fruit surface from the rooting medium (Bledsoe *et al.* 1949), a property compensating for the meagre xylem intake of the fruit.

Our studies of CO_2 fluxes between the pea fruit and its external and internal atmospheres, have enabled its photosynthetic performance to be related to the overall carbon budget of the fruit. During the first half of a 36-day growth period (Fig. 4A; 0-18 days) much of the carbon imported through the fruit stalk is consumed in pod growth, and $^{14}CO_2$ feeding studies show that pod photosynthesis is to the benefit of the pod rather than the contained seeds. At this time the pod fixes more CO_2 from the external atmosphere than from the pod gas space, largely because the respiratory output of seeds at this stage is small relative to the photosynthetic potential of the pod. In the second half of fruit development (18-36 days; Fig. 4B), pods have ceased to accumulate dry matter so translocate from the parent plant is directed entirely to seeds. Seeds also benefit from pod photosynthesis, especially the fixation of respired CO_2 from the gas cavity of the fruit.

As a result of pod photosynthesis a fully illuminated fruit of *Pisum sativum* requires over its life 16-19% less carbon from the parent plant than would a fruit laying down the same amount of dry matter in total darkness (Flinn *et al.* 1977). It follows that agronomic practices should be designed to maximise the efficiency of light interception by fruits in the plant canopy.

From the viewpoint of seed production as a nutritional source for animals the most significant measure of fruit performance is how efficiently assimilates imported from the parent plant are ultimately converted into digestible food reserves of seeds. To make such estimates we require knowledge of the weight of sugar and nitrogenous solutes imported by the fruit during its life, the final dry weight of the seeds, and the proportion by weight therein of "useful" food reserves such as starch, oil and protein.

A comparison between two species, white lupin (Pate *et al.* 1977) and garden pea (Flinn *et al.* 1977), shows how grain legumes may vary in these respects. Both of these species bleed from their phloem and xylem (Pate *et al.* 1974), so the identity of the translocated solutes received by the fruit can be accurately assessed. This information, matched against the economy of carbon, nitrogen and water of the fruit, allows one to compute the precise weights of amides, amino acids and sugars imported by the fruit during its life. As shown in the data of Table 4 the pea fruit turns out to be the more efficient converter of assimilates into seed dry matter (69% in peas, 50% in lupin), or "useful" food

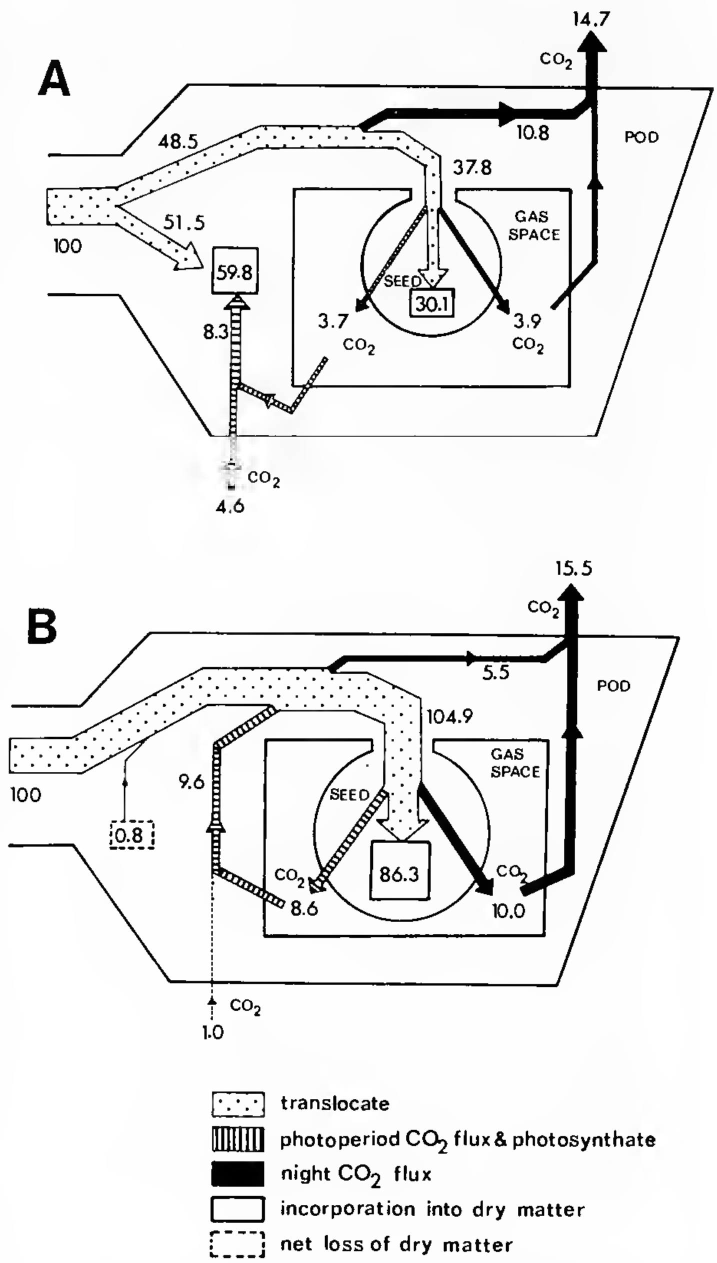

Figure 4.—Economy of carbon in developing fruits of *Pisum sativum* L. (cv Greenfeast). Carbon fluxes are shown in relation to intake of translocate and exchanges of CO_2 between seeds and pod of the internal and external atmospheres of the fruit. Daytime respiration of the fruit is not shown. (A) 0-18 days after anthesis, a period when 351 mg C were imported through the fruit stalk; (B) 18-36 days after anthesis, a period when 797 mg C were imported through the fruit stalk. The flux values in (A) and (B) are expressed relative to an intake of 100 units of carbon through the fruit stalk. (Data from Flinn *et al.* 1977).

substances (45% in peas versus 31% in lupin), but the lupin fruit emerges as the superior species if efficiency is measured in terms of production of seed protein.

Table 4.

Efficiency of conversion of translocate into seed products by fruits of two species of grain legume

	Pisum sativum L. (cv Greenfeast)	*Lupinus albus* L. (cv Neutra)
(A) Solutes translocated to fruits (mg . plant $^{-1}$)		
sucrose	2 404	1 756
amides + amino acids	393	334
(B) Materials laid down in fruits (mg . plant $^{-1}$)		
total dry matter	1 930	1 070
protein	387	412
oil	19	132
perchloric acid-soluble carbohydrate	857	110
(C) Conversion efficiency by weight of imported solutes to fruit components (%).		
to dry matter	69	50
to protein	14	19
to protein + oil + digestible carbohydrate	45	31

It remains to be seen how the values obtained by the two fruits described above compare with grain legumes as a whole, and whether better conversion efficiencies might be achieved in fruits by careful selection or breeding.

The carbon economy of whole legumes

Before judgment can be passed on the relative efficiencies with which grain legumes operate as crop plants, assessments must be made of their total performance, especially in the context of utilization of photosynthate, for nitrogen fixation and, ultimately, for seed production. With this in mind we have attempted to construct for several grain legumes budgets for carbon utilization during growth of the whole plant and its parts, utilizing information on carbon gains or losses as dry matter of plant parts, knowledge of the compounds involved in root-shoot interchange via xylem and phloem, and assessments of respiratory and photosynthetic exchanges of CO_2 by plant organs over specific intervals of the growth cycle. The budgeting takes as its centrepoint the partitioning of the net photosynthate produced by photosynthetic surfaces of the plant during the day, this quantity being determined indirectly as:—

Net photosynthate (net C gain by shoot in day) = Total C gain as dry matter by plant day and night + Respiratory loss of C from shoot at night + Respiratory loss of C by nodulated root (day + night)

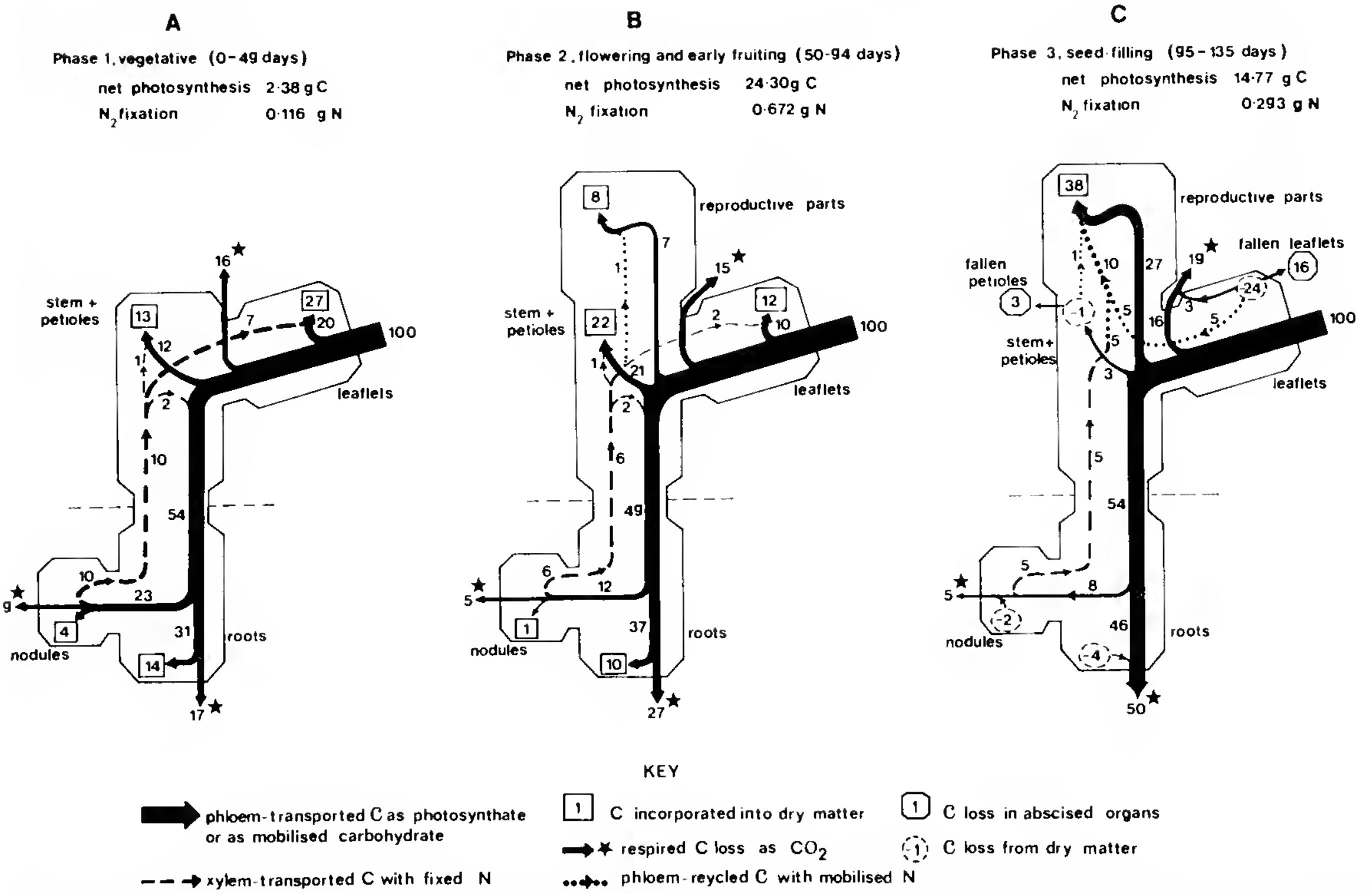

Figure 5.—The economy of carbon in nodulated plants of *Lupinus albus* L. (cv Neutra), relying solely on nodules for their nitrogen supply. The situation in three phases of the growth cycle is described. In each case items of the carbon budget are expressed relative to a net intake of 100 units of carbon by photosynthetic surfaces of the shoot. The amounts of carbon and nitrogen assimilated during each phase are indicated. (Data from Pate and Herridge 1978).

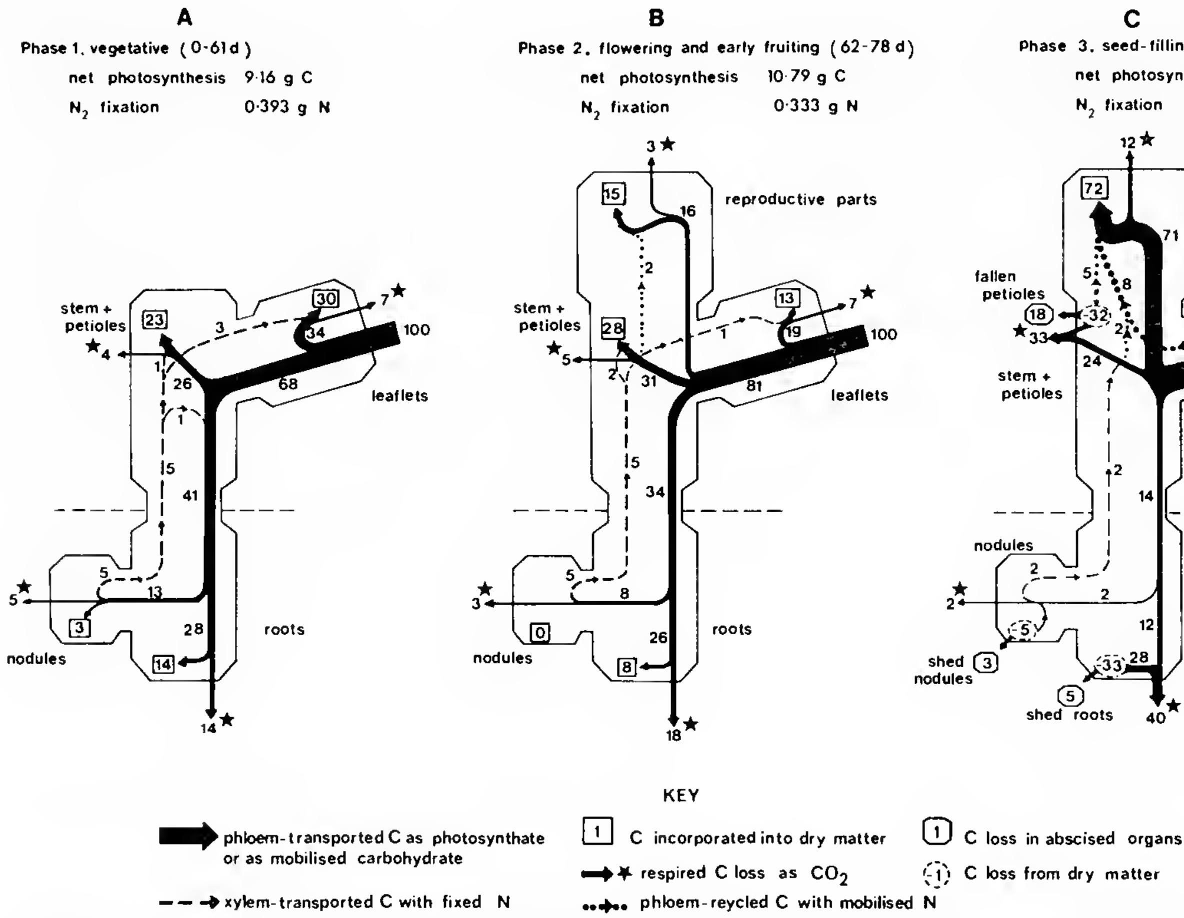

Figure 6.—The economy of carbon in nodulated plants of *Vigna unguiculata* (L.) Walp. (cv Caloona) relying solely on nodules for their nitrogen supply. The situation in three phases of the growth cycle is described. In each case items of the carbon budget are expressed relative to a net intake of 100 units of carbon by photosynthetic surfaces of the shoot. The amounts of carbon and nitrogen assimilated during each phase are indicated. (Data from Herridge and Pate 1977).

By measuring respiratory losses and dry weight changes in nodules and roots separately from those of shoots, the significance of the plant's nodules as consumers of net photosynthate can be assessed. Also, as described in an earlier section on nodule functioning, the C:N ratio of xylem exudate can be related to nitrogen increments of the shoot to estimate how much of the carbon donated to the root, as photosynthate, returns back to the shoot attached to products of nitrogen fixation.

Information is available at present for only two legumes, white lupin, a tap-rooted species, grown as a winter annual in Western Australia, and cowpea, a slender-rooted tropical legume and a summer legume as far as culture in Western Australia is concerned. The cultivars of both species used for the experiments were characterized by low harvest indices for seed production, and hence may be regarded as typical of the many legumes needing selection for improved yield of grain.

The carbon economy of these species is summarized in Figures 5 and 6, the comparisons relating to each of three stages of growth, namely vegetative development prior to flowering, flowering and early fruiting, and seed filling. Each budget expresses items of expenditure of carbon relative to a net intake of 100 units of carbon as net photosynthate by foliar surfaces of the plant. Attached to each budget is information on the amounts of nitrogen fixed and net photosynthate generated, so that the relative importance of each phase of growth is depicted relative to the total assimilatory output of the plant during its life. Comments relating to each phase of development are as follows:—

Vegetative growth.—Although the vegetative phase of lupin lasted longer and encompassed a much greater proportion of the plant's growth and assimilation than in cowpea, the species show very similar patterns of partitioning of net photosynthate. The largest single item is carbon translocated to roots (54% of net photosynthate in lupin, 41% in cowpea), most of this being respired, some contributing to growth of root and nodule, and a relatively small amount returning to the shoot associated with products of nitrogen fixation.

Flowering and early fruiting.—Both species show greatest photosynthetic and nitrogen-fixing capacities at this time. Lupin continues to acquire almost half (49%) of the plant's net photosynthate, versus one-third (34%) in cowpea. The high consumption of carbon by roots of lupin relates particularly to the establishment

and maintenance of an extensive tap-root. Whilst most desirable for growth in the dry, nutrient-poor sands of south-west Australia, this feature clearly carries penalties in terms of decreased diversion of photosynthate to grain.

The proportions of photosynthate consumed by nodules during flowering and early fruiting is less than in vegetative growth, reflecting the ever increasing sink capacity of shoots for photosynthate. Four times more carbon is bound into shoots than into nodulated roots in lupin, seven times more in the case of cowpea, so the shoot: root weight ratio widens progressively after flowering.

Seed filling.—Most marked differences occur between the species at this stage. The roots share of photosynthate remains high (54%) in lupin, but is much less (14%) in cowpea. As might be expected, returns of fixed N from nodules are lower during this phase in cowpea than in lupin, and, due to a lower expenditure of carbon on roots, cowpea is able to divert relatively more photosynthate to fruits than in lupin. However, when measured in terms of efficiency of mobilization of nitrogen to seeds, lupin proves superior, 61% of its fixed nitrogen ending up in seeds compared with only 43% in cowpea. This is because the high protein seeds of lupin incorporate relatively more nitrogen than do the low protein seeds of cowpea (see Tables 1 and 5).

Since the value of legumes stems mainly from the protein which they synthesize, the efficiency with which photosynthate is used for this purpose is a very relevant measure of their functioning as crop plants. The cultivars of cowpea and lupin examined in our investigations are used in agriculture as green forage crops as well as for grain production, so conversion efficiencies are appropriate if based on photosynthate consumption in relation to protein synthesized in above-ground vegetative parts by the time of flowering, or on the basis of protein harvested in seeds at the end of the growth cycle. The relevant calculations are shown in Table 5, where it can be seen that 17-25 g net photosynthate (as carbohydrate) are required to make each gram of protein accumulated in above ground parts by the time of flowering, 31-33 g carbohydrate for each gram of protein harvested as seed. Thus there is a conversion by weight of only 4-5.8% of the net photosynthate produced in vegetative growth into forage protein, an efficiency of only 3% for the comparable conversion to seed protein. It would be especially interesting to see how the values for the relatively unimproved cultivars studied here compare with the situation in cultivars and species of grain legumes selected for high yield of seed. Such comparisons are in progress.

It is now appropriate to return to the original question of how grain legumes compare with other seed-yielding crops in productivity and overall efficiency of performance. There simply is not yet enough data available for such comparisons to be made, since the economy of carbon in non-legumes has yet to be studied on strictly comparable grounds to our own studies of legumes, and it would indeed be most unwise to attempt to generalize about legume performance on the basis of investigations of only two species. It would seem appropriate in further studies on legumes to examine the mechanisms underlying the substantial respiratory losses which occur from roots and the processes whereby fruits and nitrogen-fixing nodules compete for a dwindling supply of assimilates at the end of the growth cycle. Our data suggest that nodules, and their fixation activities, are not particularly large consumers of photosynthate, so that any inadequacies which legumes may show in comparison with non-legumes are likely to relate to the overall performance of the host plant rather than to the symbiotic fixation of nitrogen.

Table 5.

Costs in terms of net photosynthate of protein production by two grain legumes (1)

	Vigna unguiculata (L) Walp. (cv Caloona)	*Lupinus albus* L. (cv Neutra)
(A) Synthesis of protein in above-ground vegetative parts (2).		
Production of net photosynthate (g carbohydrate . plant^{-1})	50.1	66.7
Protein accumulated in shoot (g . plant^{-1})	2.91	2.70
Net photosynthate consumed per unit of protein synthesized (g carbohydrate . g protein^{-1})	17.2	24.7
(B) Synthesis of seed protein (3).		
Production of net photosynthate (g carbohydrate . plant^{-1})	61.8	103.6
Protein accumulated in seed (g . plant^{-1})	1.90	3.34
Net photosynthate consumed per unit of seed protein synthesized (g carbohydrate . g protein^{-1})	32.5	31.0

(1) Data for cowpea from Herridge and Pate (1977) and for white lupin from Pate and Herridge (1977).

(2) Measured over the period from germination to the time of maximum nitrogen content in above-ground vegetative parts (i.e. at 79 days after germination in *Vigna,* and at 95 days in *Lupinus*).

(3) Production of net photosynthate calculated for complete growth cycle, seed protein measured as amount present per plant at full maturity (i.e. at 120 days in cowpea, and at 135 days in white lupin).

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Studies on the resin chemistry of some Western Australian plants

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Abstract

Chemical research on plant resins in Western Australia is reviewed with particular reference to components of the sub-family Ricinocarpoideae of the Euphorbiaceae. The diterpenoids are discussed in terms of their relationships with the gibberellin pathway. Separate correlations between the bicarbocyclic and tetracyclic groups are also given and in vivo experiments to define some of these relationships are described. Microbiological hydroxylation of tetracyclic systems is also summarised and an account of some experiments relating to gibberellin biosynthesis is presented. The occurrence of triterpene and flavonoid components associated with the resins is also given.

Introduction

As casual observers the late Professor White and I were particularly impressed by the frequency plant species in the Eremean and Wheatbelt areas of Western Australia exhibit resin coatings on their leaves and terminal branches. The organic chemist is aware not only of industrial applications of resins and allied substances but also of the fact that these materials have been one of the main sources of the polyterpenes. In particular the most abundant of the resins, those from pines, revealed the field of diterpenes to organic chemistry. At the outset of this work diterpenes were a small group of compounds which were largely confined to the pines and so we were interested to discover if these common coatings were a major extension of this group. As with the pine resins we were at first restricted by the problem of separating what were often complex mixtures and progress was accelerated by sampling on a wide scale and selecting the more tractable mixtures. Developments in analytical and preparative methods of separation allowed us to return later to the more complex cases which are commonly encountered, particularly in *Eremophila*. The project we began in this area is a continuing one but those aspects of it related to the sub-family Ricinocarpoideae of the Euphorbiaceae have reached the stage where they can be usefully reviewed. In view of developing interest by biologists in plant resins (Dell and McComb 1974, 1975) the opportunity is also taken to catalogue resin components from other local species. In the early stages the main problems lay in the proof of structure and stereochemistry. Advances in physical methods make these problems secondary and since they are of interest only to chemists this aspect of the work is treated briefly. On the other hand the biosynthesis of many of these substances is of general interest and in the sequel the structural patterns are identified and correlated through direct pathways although the existence of metabolic networks is most probable. A number of in vivo experiments have been carried out to define more obscure biosynthesis and these are discussed. The relationship of the *ent*-kaurene diterpenes to gibberellins is of particular importance and our contribution in this area is also summarised.

Resins from species of Ricinocarpoideae

The first material chosen came from the widespread *Beyeria drummondii* which gave ~20% of ether soluble resin of which almost a quarter was the cinnamate of a diterpenetriol with a new carbon skeleton which we called beyerane. It was clear that an extension to other members of the family was warranted and wide-ranging plant collections were undertaken to secure material. These provided many of the known species of Ricinocarpoideae along with a number of new members some of which were ultimately described at Kew (Airy Shaw 1971) through the agency of the Western Australian Herbarium. These included *Beyeria calycina* and *B. calycina* var. *minor*, *B. brevifolia* var. *truncata* and var. *brevipes*, and *Bertya cupressoidea*. Inevitably many of our early papers used undefined names and the relationship of these plants to the present taxonomy has been summarised recently (Errington *et al.* 1976). Most species of *Beyeria* and *Bertya* carried resin, exceptions being the coastal *Beyeria cyanescens* which lacked significant coating and the near-coastal *B. gardneri* which had very little. On the other hand *B. viscosa* from Rottnest Island had a substantial resin layer. No resin was observed on *Monotaxis* spp. or on *Ricinocarpus tuberculatus* or *R. velutinus* although the latter showed some toxicity which was associated with low-level anti-tumor activity. *Amperea* spp. have not been studied.

In general the resins were hard materials which consisted largely of widely varying proportions of flavonoids, diterpenes and fatty material with triterpenes appearing in *Beyeria brevifolia*, *B. viscosa* and *B. leschenaultii*. The resin of *B. brevifolia* var. *truncata* represents one extreme in that it is essentially flavonoid whereas *B. viscosa* and *B. lepidopetala* show no significant proportion of these compounds. A list of the main polyterpenoids and flavones isolated together with salient references is given in Table I.

Table 1

Chemical components of resins from species in the Ricinocarpoideae

Species	Polyterpenes (Structures)	Flavones*	References
Beyeria brevifolia (Muell. Arg.) Benth var. *brevifolia* Airy Shaw	secopimaradiene (*21*), lup-20(29)-ene-3β,16β-diol, and lup-20(29)-ene-3β,16β,28-triol	5,7,3′-trihydroxy-3,8,4′,5′-tetramethoxy-	Chow and Jefferies 1968 Errington *et al.* 1976
B. brevifolia (Muell. Arg.) Benth var. *brevipes* Airy Shaw	kauranes (*39*), (*40*)		Baddeley *et al.* 1964c
B. brevifolia (Muell. Arg.) Benth var. *truncata* Airy Shaw		5-hydroxy-7,4′-dimethoxy- 5,4′-dihydroxy-7-methoxy- 5,7-dihydroxy-3,8,4′-trimethoxy-	Dawson *et al.* 1965
B. brevifolia (Muell. Arg.) Benth var. nov.	secopimaradiene (*21*). lup-20(29)-ene-3β,16β-diol and lup-20(29)-ene-3β,16β,28-triol.	5,7,4′-trihydroxy-3,8-dimethoxy- 5,7,4′-trihydroxy-3,8,3′-trimethoxy- 5,7-dihydroxy-3,8,3′,4′,5′-pentamethoxy-	Stacey 1970
B. calycina Airy Shaw	labdanes (*10*) (*11*)(*12*/(*13*) kauranes (*8*)(*39*)(*41*)(*42*)(*45*)(*46*)	5,4′-dihydroxy-3,7-dimethoxy-	Jefferies and Payne 1965
B. calycina Airy Shaw var. *minor* Airy Shaw	beyeranes (*23*)(*25*)(*27*)(*29*) secobeyeranes (*24*)(*26*)(*30*)		Ghisalberti and Jefferies 1968, Bakker *et al.* 1972
B. drummondii Muell. Arg.	beyerol (*25*)	5,4′-dihydroxy-7-methoxy- 5,7-dihydroxy-4′-methoxy- 5,7,4′-trihydroxy-	Jefferies *et al.* 1963 Stacey 1970 O'Connell and Maslen 1966
B. drummondii Muell. Arg. var. nov.	beyeranes (*22*)(*25*)(*28*)	5,3′,4′-trihydroxy-7-methoxy- 5,3′-dihydroxy-3,7,4′-trimethoxy- 5,7-dihydroxy-3,7,8-trimethoxy-	Ratajczak 1969 Jefferies unpublished
B. latifolia (Muell. Arg.) Baill.	kauranes (*35*)(*38*)	5,4′-dihydroxy-7-methoxy- 5,7,4′-trihydroxy-	Jefferies and Retallack 1968a
B. lepidopetala F. Muell.	labdanes (*15*)(*16*)(*17*)		Coates 1966
B. leschenaultii (D.C.) Baill.	kauranes (*31*)(*35*)(*38*)(*43*)(*46*)(*48*) lup-20(29)-ene-3β,16β-diol	5,4′-dihydroxy-3,7,8-trimethoxy-	Jefferies and Retallack 1968b Baddeley *et al.* 1964a,b
B. viscosa (Labill.) Miq.	kauranes (*31*)(*32*)(*33*)(*34*)(*35*)(*36*) (*37*)(*42*) lup-20(29)-ene-3β,16β-diol lup-20(29)-en-3-one		Coates 1966
Bertya cupressoidea Airy Shaw	bertyadionol group (*50*)(*51*)		Ghisalberti *et al.* 1974 Maslen *et al.* 1975
B. dimerostigma F. Muell.		5,3′,5′-trihydroxy-3,7,4′-trimethoxy-	Henrick and Jefferies 1964b
Ricinocarpus muricatus Muell. Arg.	labdanes (*14*)(*15*)(*16*)(*17*)(*18*)(*19*)	5,7,3′,4′-tetrahydroxy-3,8-dimethoxy- 5,3′,4′-trihydroxy-3,7,8,-trimethoxy- 5,3′-dihydroxy-3,7,8,4′-tetramethoxy-	Henrick and Jefferies 1965a, 1965c
R. psilocladus (Meull. Arg.) Benth.		5,7,3′,4′-tetrahydroxy-	Stacey 1970
R. stylosus Diels	polyalthic acid (*20*); kauranes (*8*)(*41*)(*43*)(*44*)(*45*)(*47*)	5,4′-dihydroxy-3,7,8-trimethoxy- 5,3′-dihydroxy-3,7,8,4′-tetramethoxy- 5-hydroxy-3,7,8,3′,4′-pentamethoxy-	Henrick and Jefferies 1964a 1964b, 1965b

* For numbering see Figure 8b.

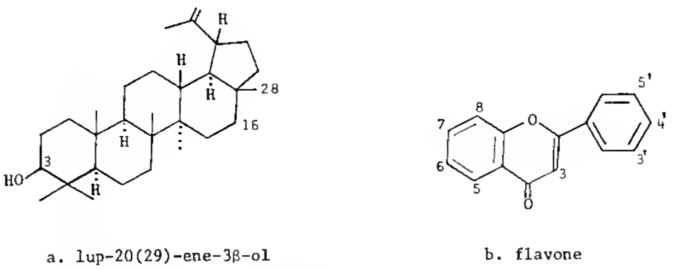

Figure 1.—A.- lup-20(29)-ene-3β-ol. B.- flavone.

Beyeria brevifolia, B. viscosa and *B. leschenaultii* provided large quantities of the triterpene lup-20(29)ene-3β, 16β-diol, which in the latter plant was associated with a small proportion of the 3β,16β,28-triol. Despite the fact that lup-20(29)-ene-3β-ol (Fig. 1a) and the 3β,28-diol are very widely distributed in plants neither the 3β,16-diol or the triol had been isolated previously. Evidently 16β-hydroxylation of the 3β-ol is an abberration of the hydroxylating system deflecting attack from C-28 to the neighbouring C-16. The structures of these triterpenes were proved by interrelation with each other and with known lupane derivatives.

Despite the fact that the flavones (Fig 1b) are widely distributed and well documented most of the substances we isolated were new members of the class. The resin flavonoids are exceptional in that not only are they highly methoxylated but they frequently occur as a large proportion of the plant material. A number of common structural features were observed and these include the ubiquitous 5-hydroxyl group and the fact that when substitution occurs at C-3 or C-8 then the substituent is always methoxyl. Oxygenation of the A ring follows the normal 5,7 pattern, established by assembly of malonyl CoA residues and later substitution is limited to C-8; the common alternative C-6 is not substituted. Substitution of the phenyl ring follows the normal patterns 4'; 3', 4'; 3', 4', 5'. In non-resin flavones methylation of B ring hydroxyl groups occurs almost exclusively for the 3'-OH and an enzyme system effecting this reaction has been characterized (Ebell *et al.* 1972). No such specificity is observed in the resins and both the 3' and 4'-OH frequently show methylation. Many roles have been suggested for flavonoids in plants (McClure 1975) and some of these functions no doubt apply in the resins. Thus the ability to absorb UV light enhances the protective nature of the coating. They may also protect the resin from microbial attack and as well, act as antioxidants to stabilise the resin.

In considering the chemistry of the diterpenoid constituents it is useful to relate them to the biosynthesis of this group (Fig. 2). It is now well established (e.g. Hanson 1972) that diterpenes along with the steroids and triterpenes arise from acetate through mevalonate leading to the C_5 pyrophosphates which provide geranyl pyrophosphate. Successive elimination-addition reactions of two isopentenyl pyrophosphate molecules then gives geranyl geranyl pyrophosphate which with some stereochemical limitations may be considered to follow divergent paths to macrocyclic ring systems such as casbene and the cembrenes, undergo cyclisation of the three terminal C_5 residues to give C_{20} analogues of the sesquiterpenes, or the all *trans* isomer may undergo cyclisation to give the bicyclic labdane ion *(1)**. Backbone rearrangement of (*1*) gives members of the *ent*-clerodane group whereas deprotonation provides copalol pyrophosphate (*2*). The latter may cyclise first to the tricyclic pimarene (*3*)

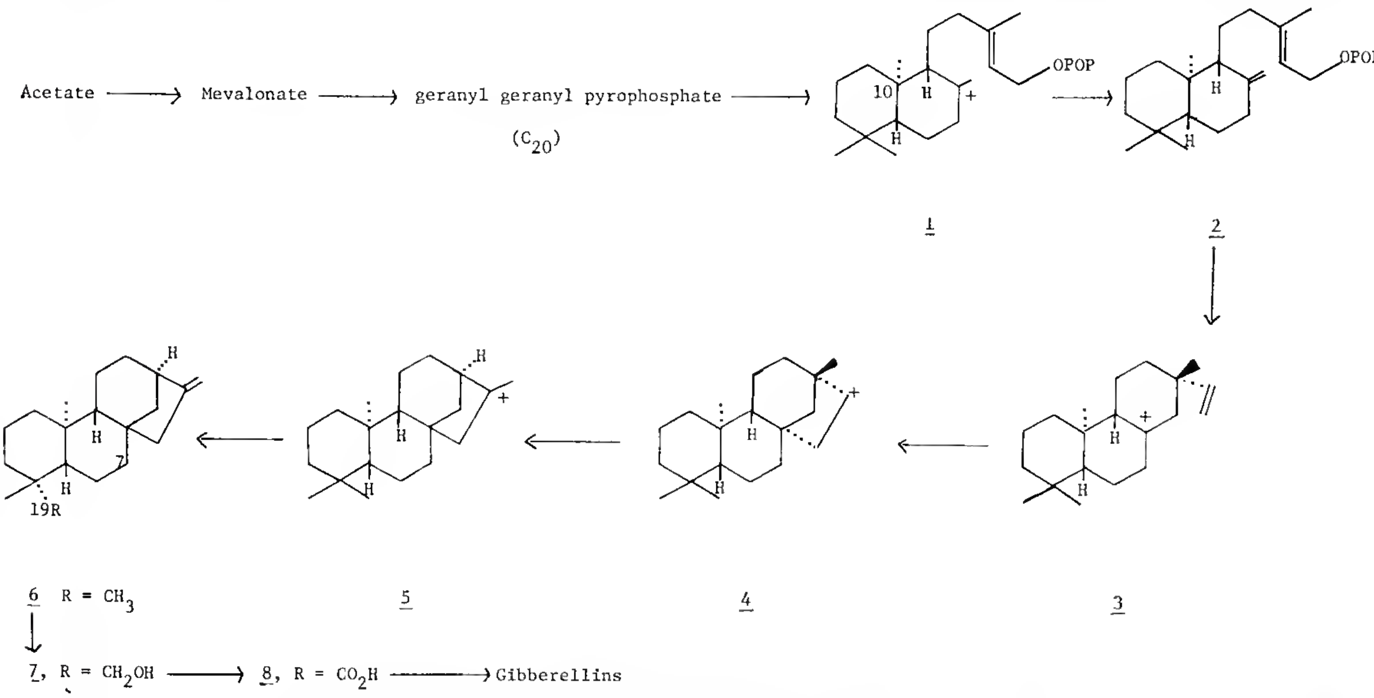

Figure 2.—Scheme for the biosynthesis of some *ent*-diterpenes.

* Numbers in parenthesis refer to structures in the figures.

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and then to the tetracyclic beyerane (*4*) and kaurane ions (*5*). The pathway is drawn to show free carbonium ions and although such species have not been proved to arise in biological systems they represent a convenient basis for rationalising the structural assembly. *Ent*-kaurene (*6*) is converted by way of the 19-hydroxy derivative (*7*) to the kaurenoic acid (*8*) which undergoes 7β-hydroxylation before generating gibberellins. In view of the wide-spread distribution of these latter compounds and their physiological role, the pathway to gibberellins may be regarded as part of primary metabolism in plants. The section from the bicyclic carbonium ion pyrophosphate (*1*) to kaurenoic acid (*8*) is a useful framework for discussing the diterpenes of Ricinocarpoideae since with the exception of the bertyadionol group, which are present in *Bertya cuppressoidea*, all can be regarded as deriving from intermediates on this pathway. The diterpenes of many other species are similarly derived. It is noted specifically that the stereochemistry of C-10 in this series is enantiomeric to that in the steroids, triterpenes and common pine resin acids. For the diterpenes, divergence occurs for the cyclisation of geranyl geranyl pyrophosphate which can give either the bicarbocyclic labdane (*1*) or its mirror image.

Bicarbocyclic diterpenes

The bicarbocyclic ion (*1*) is the parent of a wide range of substances which were obtained and rational pathways linking them, together with their distribution among the species are shown in Fig. 3. Hydration of *1* and pyrophosphate hydrolysis gives the diol (*10*) and this or the pyrophosphate are the logical precursors of the epimanoyl oxide (*11*) its 18-hydroxy (*12*) and carboxy derivatives (*13*) all four of which are found in *B. calycina*. The presence of a reductase generating the 13S configuration appears in both *B. lepidopetala* and *Ricinocarpus muricatus* leading from *10* to the diol (*14*) present in the latter, and then by hydroxylation of C-18 to the triol (*15*) found in both. Low specificity is indicated for the 13S reductase since both plants give 13S systems which arise from *9*. Thus reduction of *9* and hydroxylation and oxidation of C-18 or C-18 and C-15 give the carboxylic acids (*16*) and (*17*) respectively. Further hydroxylation of the hydroxy acid (*16*) occurs at C-16 to give the dihydroxyacid (*18*) found in *R. muricatus*. Polyalthic acid (*20*) in *R. stylosus* and the butenolide (*19*) in *R. muricatus* must arise by hydroxylation of C-16 at the 13-ene level coupled with further oxidation of the C-15 alcohol to the aldehyde in the former case and to the acid

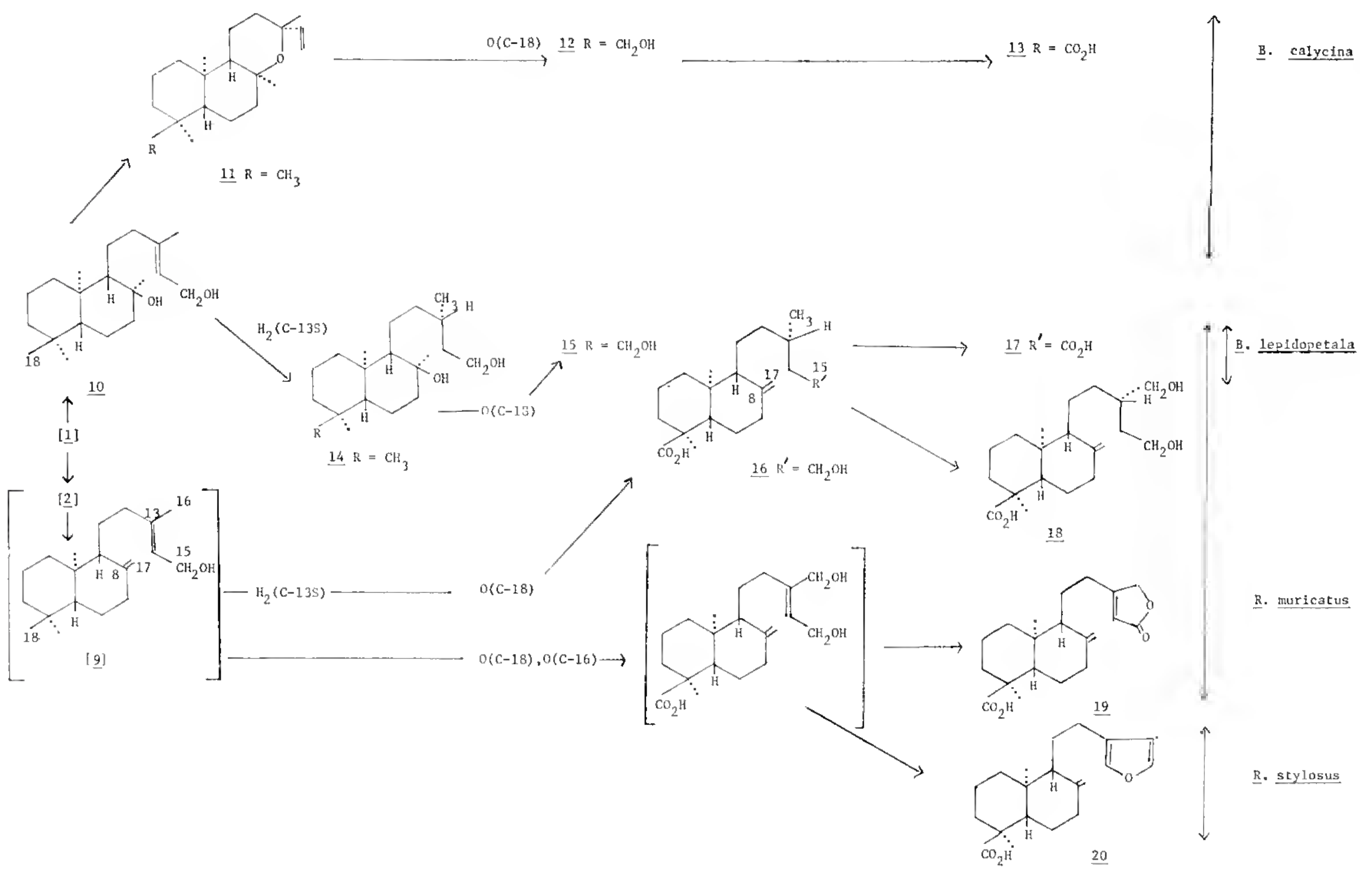


Figure 3.—Probable biosynthetic relationships of the bicarbocyclic group.

in the latter. The intermediate enediol group has been observed in diterpenes from *Sciadopitys* (Sumimoto *et al.* 1964). The hydroxylation and oxidation of C-18 in (*19*) and (*20*) might occur at any stage.

The chemical proof of the skeleton of these compounds is based ultimately on chemical interconversion with each other and with materials of known constitution, and positions of the hydroxyl and carboxyl groups follow largely from spectroscopic and pK measurements. The main ambiguity which required resolution was the configuration of the C-13 position. This was shown to correspond to that of eperuic acid which was however unsettled. We were able to clarify this situation (Henrick and Jefferies 1965a) since compounds with the 13R configuration were available to us from simultaneous research on *Dodonaea lobulata* resin (Dawson *et al.* 1966). That these were epimeric at C-13 with those from *Ricinocarpus* followed from the laboratory preparation of both from the diol (*10*). Within the various groups of polycyclic diterpenes oxygenation occurs commonly at either C-18 or C-19. The bicarbocyclic examples listed above show oxygenation at C-18 and not C-19, in sharp contrast with the tetracyclics described below, which exhibit oxygenation of C-19.

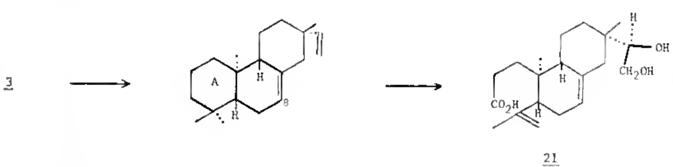


Figure 4.—Origin of the seco-pimaradiene (*21*).

Tricarbocyclic diterpenes

The families of tricarbocyclic diterpenes derive from a stereoisomer of the intermediate ion formally shown as *3*. *Beyeria brevifolia* var. *brevifolia* and an undescribed variety both generate compounds based on this skeleton. The resin of the former contains mainly one diterpene (*21*, Fig 4) obtained as ~5% of the leaves and branchlets. The efficient production of *21* is noteworthy since evidence presented in the sequel suggests that it is apparently at least four steps from the main path. Thus after formation of the 8-ene from *3*, hydroxylation of both C-3 and C-19 are evidently required before fragmentation of the A-ring can occur. Analogous A-ring splitting is seen in *Beyeria calycina* var. *minor* but has not been reported for other diterpenes although several examples are known in the triterpenes. Hydroxylation of the vinyl group could occur at any stage and is analogous to the 16,17-dihydroxylation of kaurene discussed below. The structure assigned to *21* follows from its interconversion with a derivative of beyerol.

Beyeranes

The diterpenetriol (*25*, Fig. 5) from *B. drummondii* proved to have a new carbon skeleton which was called beyerane and was recognised as the missing link (*4*, Fig. 2) in the formal pathway from the tricyclic ion (*3*) to kaurene. The structure was proved largely by classical oxidative degradation and dehydrogenation with the limited application of physical methods and the absolute stereochemistry was shown to be antipodal to the steroids by optical rotatory dispersion methods. Small quantities of the diols (*22*) and (*28*) were also isolated from a variant.

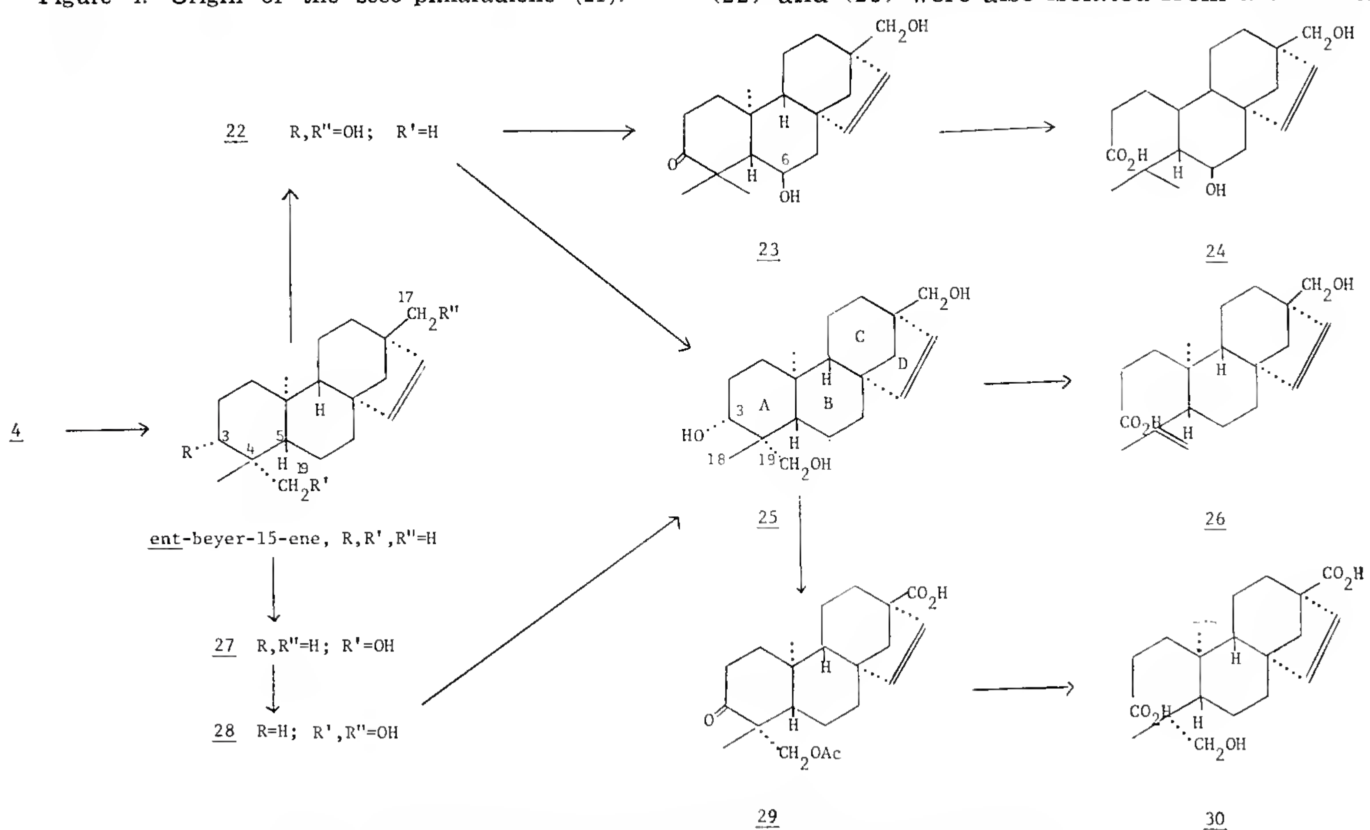


Figure 5.—Probable relationships between *ent*-beyerene metabolites.

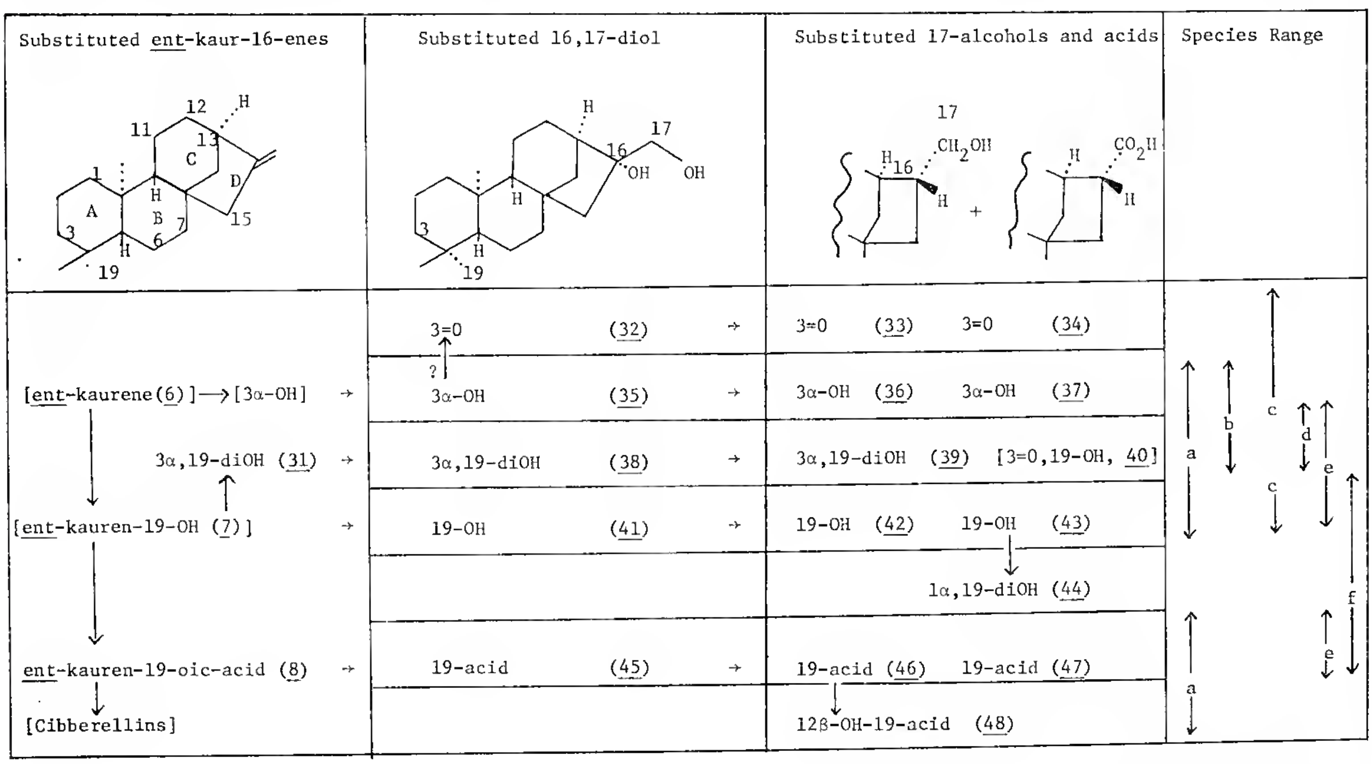
Beyeria calycina var. *minor* provided a group of beyerene metabolites of which the more abundant are the 6-acetate of the ketodiol *(23)* and the seco-acid *(26)* which has undergone A-ring fission analogous to the pimaradiene *(21)*. Several methods of effecting this ring splitting have been developed in the laboratory. Thus photolysis (Arigoni *et al.* 1960) of 3-ketones, as for example *23*, gives rise to the acids *(24)* bearing an isopropyl group as an A-ring fragment. Acids in which this residue appears as isopropenyl *(26)* can be obtained by several routes including the abnormal Beckman rearrangement (Witham 1960) of oximes of 3-ketones such as *(23)*. Both these methods were used to relate beyerol *(25)* to the seco-acid *(26)*. A biomimetic fragmentation based on the reduction of 3-keto-19-tosylates was also developed (Ghisalberti and Jefferies 1968).

Several schemes had been proposed to account for the fragmentation process in vivo although no experimental evidence in living systems was available. These schemes fell into groups either requiring C-18 and C-19 as methyl groups or those for which one of these was hydroxylated with variations within the groups arising from different oxidation states of C-3. It seemed likely that some distinction between these mechanisms might be made by feeding both *ent*-beyer-15-ene and *ent*-beyer-15-ene-19-ol *(27)* to intact plants since 19-hydroxylation is unlikely to be reversible. Seedlings of *B. calycina* var. *minor* were readily available following a bushfire and these were transplanted to a glasshouse where rapid growth occurred with regular watering. Resin production was not obviously inhibited and the normal resin components were found to be present. ^{3}H labelled samples of *ent*-beyer-15-ene, *ent*-beyer-15-ene-19-ol, *(27)*, and the 3α,19-;19,17- *(28)* and 3α,17-diols *(22)* were prepared and fed to these plants. We observed incorporation into *26* for all substrates, clearly indicating that the 4,4-dimethyl group is not essential for the fragmentation and that mechanisms based on 3,19-dioxygenated substrates are more probable (Bakker *et al.* 1972, Sefton 1978).

Beyeria calycina var. *minor* also contains small quantities of the seco-acids *(24)* and *(30)* which could be obtained independently by ultra-violet irradiation of the co-occurring 3-ketones *(23)* and *(29)* respectively. The possibility that these acids arise in the plant resin by lengthy exposure to sunlight is supported by our observation that during the short periods required for incorporation of radioactivity from the labelled substrates into *26* no significant radioactivity was detected in *24*. The retention of configuration at C4 in the sequence *29* → *30* although expected for a bio-transformation was not predicted for the photochemical reaction and is attributed to restriction to rotation of the C4-C5 bond.

Kauranes

Many of the plants we examined were found to contain metabolites of *ent*-kaurene *(6)*. The carbon skeletons of these substances were estab-



a *Beyeria leschenaultii*; b *B. latifolia*; c *B. viscosa*; d *B. brevifolia* var. *brevipes*

e *B. calycina*; f *Ricinocarpus stylosus*.

Figure 6.—Probable relationships between *ent*-kaurene metabolites.

lished by interconversion with each other and with the parent *ent*-16β-kaurane whose structure and stereochemistry had previously been resolved. A major problem in effecting these interconversions lay in the unsatisfactory deoxygenation methods available, particularly for hindered primary alcohols, and for this purpose we developed a technique involving the formation of benzyl thioethers from sulphonate esters using dipolar aprotic solvents (Henrick and Jefferies 1964a). Desulphurisation of these ethers to give the hydrocarbons proceeded smoothly.

A schematic relationship showing possible pathways between the oxygenated kaurenes is shown in Figure 6 together with the range of compounds associated with each species. Branching from the gibberellin pathway occurs by hydroxylation at C-3 of either *ent*-kaurene (*6*) or the kaurenol (7) but this is not observed for the kaurenoic acid (*8*). It is noted that C-3 and C-19 are similarly situated with respect to the D ring polar alkene group and since it is evident from microbiological hydroxylation of steroids (Jones 1973) that the distances from the binding sites control sites of hydroxylation it appears that the C-3 oxygenase and kaurene C-19 oxygenase have similar spatial demands. The C-3 and C-19 oxygenase activities operate independently since *R. stylosus* and *B. calycina* are deficient in the former and *B. viscosa* has the latter inhibited whereas the other species exhibit both about equally. The 3-and or 19-oxygenated kaurenes apparently can then undergo an unspecific hydroxylation of the double bond leading to 16, 17- diols. If hydroxylation of C-3 and C-19 is dictated by binding to the D ring double bond and if it is assumed that a binding site may in turn become a hydroxylating site (Jones 1973) then the C-3 and the C-19 hydroxyls might direct D ring hydroxylation. In the beyerenes this could explain C-17 hydroxylation and in the kaurenes 16,17-dihydroxylation can be rationalised similarly since it has been shown in metabolism of steroids by certain moulds that substitution of a saturated hydroxylation site by a double bond can lead to an epoxide (Bloom and Shull 1955) and the latter can readily generate a 1,2-diol. The formation of these 16,17-diols appears to be general and serves incidentally to remove kaurenol (7) and kaurenoic acid (*8*) from the gibberellin pathway. An alternative fate for the 16-ene is the formation of either the C-17 hydroxy or carboxy derivative, through steps which appear to be available to most plants examined and which permit a wide choice of substrate. Evidence presented below indicates that these substances derive from sequences analogous to the pinacol rearrangement and probably arise through the diol directly or the intermediate epoxide. In either case the aldehyde is the immediate product and this can distribute itself betwen primary alcohol and carboxylic acid. The major kaurene metabolites are thus accounted for. Two minor components are the 1α,19-dihydroxy-17-acid (*44*) which co-occurs with the 19-hydroxy-17-acid (*43*) in *R. stylosus* and the 12β,17-dihydroxy-19-acid (*48*) which co-occurs with the 17-hydroxy-19-acid (*46*) in *B. leschenaultii*. These products can be rationalised as arising from the third binding site of the hydroxylating system. Thus primary binding to the C-19 carboxyl with secondary binding to C-17 H_2OH is assumed to direct the third site to C-12β. Primary binding to C-17 carboxyl with secondary attachment C-19 H_2OH could then result in C-1α hydroxylation since the C-17 → C-12 and C-1 → C-19 distances are similar.

In summary then in its simplest terms the secondary metabolism process in Figure 5 can be explained by the operation of one hydroxylating system with three binding hydroxylating sites along with an isomerase responsible for the rearrangement of the 16,17-diols leading to C-17 alcohols and acids.

The formation of acid and primary alcohol functions at C-17 has little biological precedent and warranted further study (Croft *et al.* 1978). Five possibilities which may be considered are shown in Figure 7. Mechanism (a), an anti-Markovnikoff hydration has been postulated for a similar conversion of *ent*-kaurene in barley seeds (Murphy and Briggs 1973). Mechanisms (b_1) and (b_2) involve pinacolic rearrangements either through the epoxide or its diol and have strong chemical analogy. Mechanism (c) has its analogue in the dioldehydrase reaction and permits such exchange of H_1 on the enzyme complex (Frey and Abeles 1966). Mechanism (d) involves a dehydratase reaction leading to an enol. The mechanisms predict four different fates for the vinyl protons in *8* during its transformation to

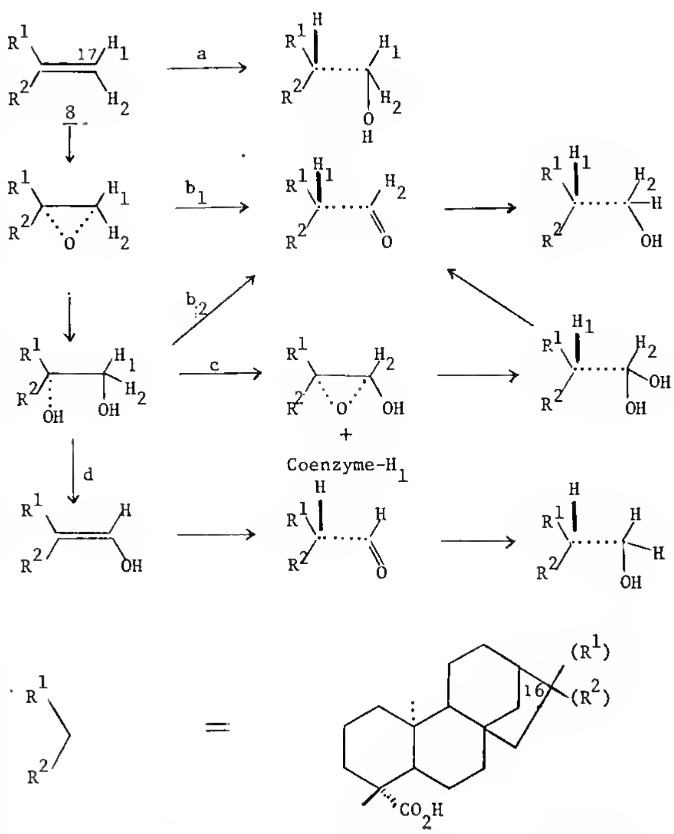


Figure 7.—Mechanisms for the biosynthesis of the hydroxy acid (*46*) from *ent*-kaurenoic acid (*8*).

46. To distinguish these mechanisms kaurenoic acid labelled with ^{14}C and ^{3}H at C-17 was prepared and fed to seedlings of *B. calycina*. The results show that no tritium was lost thus excluding mechanisms (c) and (d), and that about half of the tritium had migrated to C-16 consistent only with mechanisms of type (b). Distinction between routes (b_1) and (b_2) has not been made.

Diterpenes of Bertya cuppressoidea

It has recently become clear that a number of species of Thymeleaceae and Euphorbiaceae, particularly *Euphorbia* and *Croton* produce diterpenes which do not derive from the bicyclic ion *1*. Some of these are potent co-carcinogens, of which the esters of phorbol (*54*, Fig. 8) are best known (Hecker and Schmidt 1974).

The pathway to the carbon skeleton of phorbol has not been established but clues to a likely route are provided on the one hand by the structures of the *Bertya* diterpenes (Ghisalberti *et al.* 1973a, 1974) and by the related lathyrol group (Opferkuch and Hecker 1973) and on the other by casbene *(49)*. The latter is produced by an enzyme preparation of *Ricinus communis* (Euphorbiaceae) acting on geranyl geranyl pyrophosphate (Robinson and West 1969). Bertyadionol *(51)* is the most abundant diterpene of *Bertya cuppressoidea* and co-occurs with diterpene-D (50) and -B, the C9-ene. The structures were assigned by interrelation with each other, coupled with extensive spectroscopic studies and the absolute configuration was established by oxidation to R-methylsuccinic acid and to the cyclopropane derivative homocaronic acid. The structural relationships between the *Bertya* diterpenes strongly suggest that the five-membered ring results from aldol condensation of a diketone, which could be formed by allylic oxidation of casbene at C-8 and C-11, resulting in a C7-C11 bond. Oxidation of C-4 and C-12 would then provide diterpene D and bertyadionol. Diterpene B could arise similarly with retention of the 9-ene after inversion to the Z configuration. Further cyclisation of this skeleton to give the phorbol ring system requires linking C-12 and C-3, perhaps by an aldol type cyclisation promoted by the C-5 substituent at the aldehyde level (Worth 1971).

Bertyadionol has anomalous UV absorption suggesting interaction between the cyclopentenone and vinylcyclopropylenone chromophores. Irradiation of bertyadionol with UV light readily affords a photo product as a consequence of an unprecedented sequence leading to structure (*52*) (Ghisalberti *et al.* 1978a). The photoproduct (diterpene C) accompanies bertyadionol in the plant extracts and is probably formed in the surface resin by solar radiation. Photolysis of diterpene-D (*50*) results in an isomer (*53*) in which the 13-ene has undergone the unexceptional E-Z isomerisation. The inversion of C-2 which also occurs is probably due to ring fission generating a C-15 carbene, rotation of the C-1:C-2 bond and recyclisation as indicated in Figure 8.

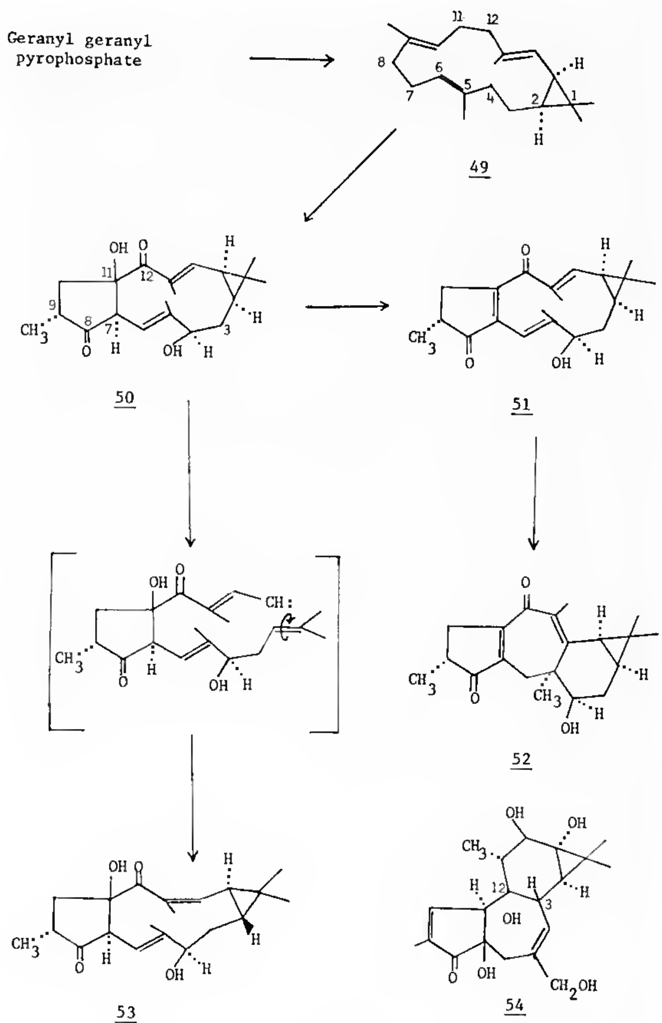


Figure 8.—Relationships between the *Bertya* diterpenes.

Mould metabolism of kauranes and beyeranes

Formal analogy between the plant and mould hydroxylating systems prompted us to carry out a survey (Beilby *et al.* 1973) of the microbial hydroxylation of a group of tetracyclics using the micro-organisms *Calonectria decora, Rhizopus nigricans* and *Aspergillus ochraceous* for which much data had been obtained on steroids by the Oxford group (Jones 1973). It was hoped on the one hand that plant hydroxylation patterns might be reproduced by appropriate mould-substrate choice and on the other we expected that the moulds in offering a wider range of hydroxylation systems might provide easy access to B and C ring hydroxylated derivatives which were not readily available from natural sources. As it turned out both expectations were realised in part (Table 2). Thus naturally occurring 1-hydroxykauranes which may be precursors of the skeleton of the grayanotoxins occur rarely but are easily available from 16,19-dioxygenated norkauranes using *R. nigricans*. Hydroxylation at C-13 is widespread in plant gibberellins but otherwise rare in natural kauranes. This step can be effected with some 16,19-dioxygenated substrates using *A. ochraceous* and although the yield is low it is comparable to synthetic procedures and much more convenient.

Table 2

*Metabolism of some kaurenes by moulds**†

Substrate	Substrate modifications		
	Calonectria decora	*Rhizopus nigricans*	*Aspergillus ochraceous*
ent-kaur-16-en-19-oic acid (**8**)	7α-OH; 15α-OH; 7α, 15α-diOH	7β-OH; 16α,17-diOH	16α,17-diOH
oxygenated *ent*-16-nor-kaur-16-ones i 3α-OH	7α-OH	1α-OH; 7α-OH	6β-OH; 7αOH
ii 19-acid	7α-OH; 7β-OH; 1α-OH	7α-OH; 7β-OH; 1α-OH	13-OH; 13,16β-diOH
iii 19-OH	7α-OH; 1α-OH	7α-OH; 1α-OH	7α-OH; 16β-OH

*Beilby *et al.* 1973; Ghisalberti *et al.* 1977a. † For numbering see Figure 6.

Hydroxylation of the B ring of kaurene is prerequisite to gibberellin formation and although no B ring oxygenated metabolites of kaurene were observed in the resins 6-oxygenated beyeranes were isolated. A number of beyerane derivatives underwent 6β-hydroxylation using *C. decora* and similarly this hydroxylation technique was used to establish the skeleton of the dihydroxy acid (*29*) (Fig. 4) since the derived triol could also be obtained from the metabolism of the diol from the authentic beyerane (*27*) (Sefton 1978). All three moulds effected 7β- and 7α-hydroxylation with a wide range of kaurane derivatives and application of these and similar methods provided a simple route to 7β-hydroxykaurenoic acid (Croft *et al.* 1974), the gibberellin precursor otherwise available only by lengthy procedures. The hydroxylation by *C. decora* of kaurenoic acid gives the 15α-hydroxy derivative a process which also occurs in the plant *Phebalium rude* which contains both these substances. Another example of plant hydroxylation effected by moulds is the formation of the 16,17-diol by *A. ochraceous* from kaurenoic acid.

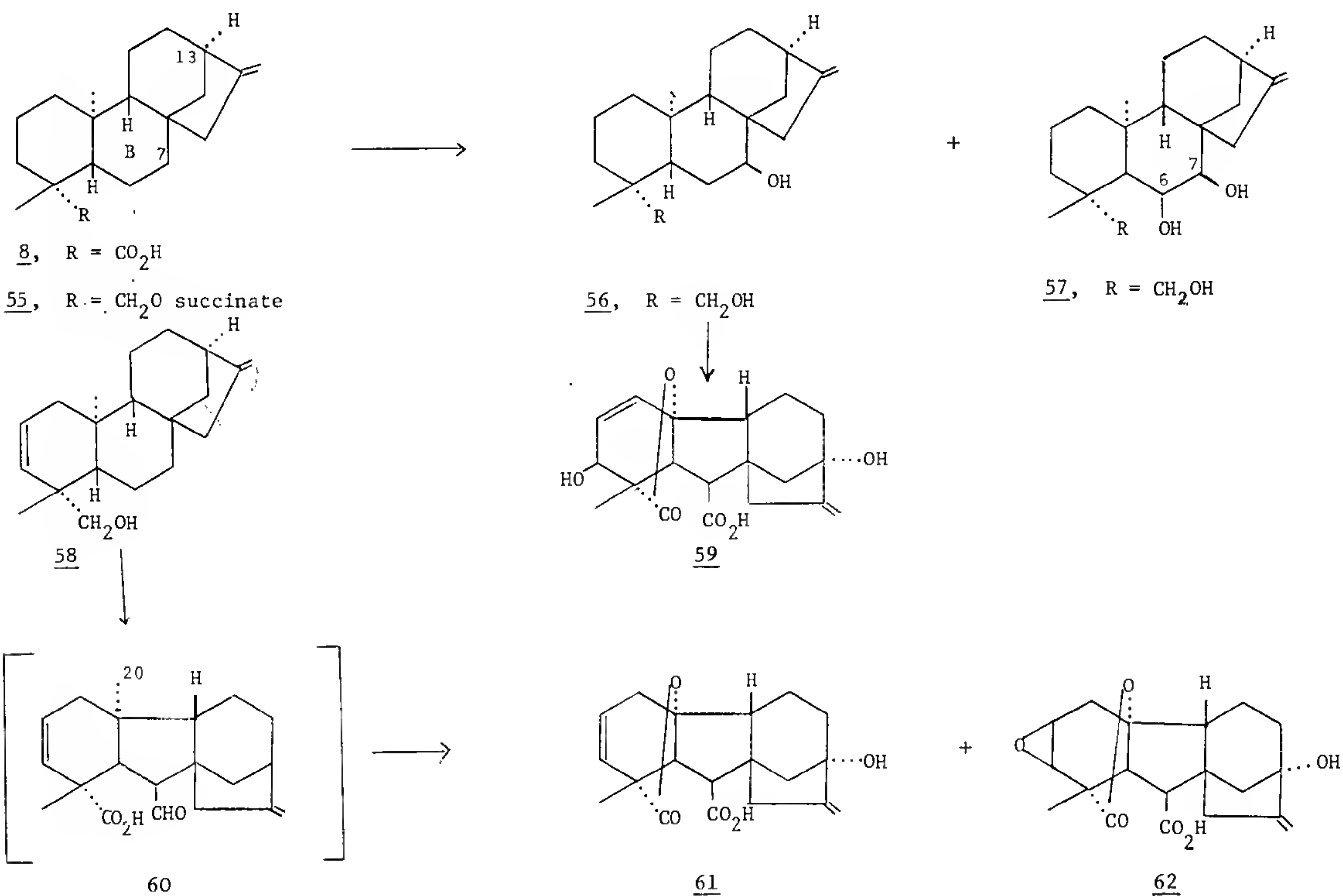


Figure 9.—Metabolism of some *ent*-kaurenes by *Gibberella fujikuroi*.

Ent-kaurenes as sources of gibberellins

When kaurenoic acid (*8*) was first obtained a report had just appeared indicating that its 13-hydroxy derivative, steviol showed gibberellin activity (Ruddat *et al.* 1963) and accordingly a joint programme was established with Dr. B. O. Phinney to determine the extent of this bioactivity within our group of kaurene metabolites. Although it was found that the effect was not general for the kaurane nucleus *ent*-kaurene (*6*), *ent*-kaurenol (*7*) and *ent*-kaurenoic acid (*8*) did behave as gibberellins in a group of dwarf maize mutants (Katsumi *et. al.* 1964a, 1964b). Since *ent*-kaurene itself was known to be a precursor of gibberellic acid it seemed likely that these substances were not intrinsically active but were converted to gibberellins during assay. This proposition was supported by feeding experiments in *Gibberella fujikuroi* by several groups using material of Western Australian origin (Graebe *et al.* 1965, Verbiscar *et al.* 1967). The sequence *ent*-kaurene → kaurenol → kaurenal → kaurenoic acid → gibberellins which emerged from this work was supported by work with plant systems (Dennis and West 1967). The formation of gibberellins from *ent*-kaurenoic acid (*8*, Fig 9) clearly involved oxidation of ring B but despite some effort the appropriate metabolite had not been obtained and so a number of kaurene derivatives were fed to *G. fujikuroi* in the hope that the hydroxylation patterns obtained would identify the next step. The results implicated C-7β-hydroxylation since this occurred in all cases (Jefferies *et al.* 1970, 1974c). Thus metabolism of the succinate ester (*55*) of *ent*-kaurenol gave the 7β- and 6β,7β-hydroxylated esters (Fig. 9). This experiment was repeated with the isotopically labelled kaurenol ester (*55*) and the 7β-hydroxy ester formed was hydrolysed to give the 7β,19-diol (*56*) which was found to be a precursor of gibberellic acid (*59*). *Ent*-kaurene-6β,7β,19-triol (*57*) which was also formed from the succinate (*55*) did not produce gibberellic acid in the mould although it possesses gibberellin activity. In the meantime other groups had reached the same conclusions (Hanson *et al.* 1972, Cross *et al.* 1970).

One apparently unnatural kaurene which shows activity in maize is the dienol (*58*). When metabolised by *G. fujikuroi* this substance gives a series of C-19 and C-20 gibberellins indicating pathways to gibberellin A_5 (*61*) and A_8 (*62*) (Bakker *et al.* 1974) neither of which are normal mould metabolites but are limited naturally to plants. Backfeeding experiments showed that the epoxidation step was probably most active for the aldehyde (*60*) level of C-7 which was also implicated in the removal of C-20.

Resins of other species

A selection of the many species outside the Euphorbiaceae which carry resin has also been studied and the results, with salient references, are summarised in Table 3. A number of plants are included which appear to lack external resin but either contain diterpenes in significant quantity or belong to genera which do.

Several *Acacia* spp. are viscid and the diterpenes of *A. rossei* have been characterised as bicyclic compounds arising from rearrangement of the ion (*1*). The presence of kaurenoic acid (*8*) and its 15α-hydroxy derivative in *Phebalium rude* is a rare case of the isolation of diterpenes from members of Rutaceae. On the other hand many Western Australian species in this family produce eriostoic or eriostemoic acid (Duffield *et al.* 1962) both of which resemble diterpene acids in the possession of twenty carbon atoms, a carboxyl group and a polycyclic skeleton. Perhaps they fulfill similar roles.

Reference has already been made to labdanes in *Dodonaea lobulata* and similar compounds were found in *D. alternifolia* and *D. ptarmicifolia*. Backbone migration in the ion 1 (Scheme 1) gives the *ent*-clerodane skeleton which is the basic structure of the compounds from several other *Dodonaea* spp. Resin is commonly seen on some members of the Boraginaceae and of these *Halgania lavandulacea* has a heavy coating and was selected for study. The resin was found to be essentially a mixture of simple flavones.

Within the Discrastylidaceae the decorative *Cyanostegia angustifolia* was found to be another source of *ent*-clerodanes. *Pityrodia lepidota* has a similar component whose relative configuration was deduced by X-ray methods. The resin of *Newcastelia viscida* contains an isopimara-9(11),15-dienediol which is the only example we have encountered which has been shown to belong to the so called normal series (C-10β CH_3) which corresponds to biosynthesis through structures enantiomeric with those of Figure 1. The stereochemistry of this compound coupled with the 9(11)-double bond suggests that it might arise from anomalous folding of geranyl geranyl pyrophosphate leading to a *trans, syn* stereoisomer of ion 1.

Eremophila species are probably the most abundant resin plants of the Eremean and have been found to contain a great diversity of diterpene skeletons. The compounds we have isolated do not evolve from the ion *1* but are either macrocyclic cembranoids or are generated by sesquiterpene type cyclisations involving the three C-5 residues adjacent to the pyrophosphate of a geranyl geranyl pyrophosphate. Although most of the resins contain significant quantities of fatty material these rarely dominate. *Myoporum beckeri* is exceptional in that its very sticky coating is largely fatty acids and alcohols. *Eremophila oppositifolia* has internal viscid material which contains a branched triply unsaturated fatty acid.

Two *Goodenia* spp. have also been examined and both contain esters of the kaurene-3α,19-diol (*31*) previously obtained from *B. leschenaultii;* indeed *G. strophiolata* is the best source of 3,19-functionalised kaurenes. One member of the Asteraceae which has been well studied is the perennial *Olearia muelleri* whose resin is another source of *ent-clerodanes*. The low level antitumour activity of this plant is associated with flavone components.

Table 3

Chemical components of other resinous and allied species

Plant Species	Polyterpenes, Fatty Acids	Flavones (or Aromatics)	References
MIMOSACEAE—			
Acacia rossei F. Muell.	(8,10)-friedolabdanes	5-hydroxy-7,4′-dimethoxy-	Langley 1966
RUTACEAE—			
Phebalium rude Bartl.	kaurenoic acid (*8*) 15α-hydroxykaurenoic acid	....	Cannon *et al.* 1966
SAPINDACEAE—			
Dodonaea inaequifolia Turcz.	*ent*-labdanes	....	Payne unpublished
D. lobulata F. Muell.	*ent*-labdanes	5-hydroxy-3,6,7,4′-tetramethoxy	Dawson *et al.* 1966
D. ptarmicifolia Turcz.	*ent*-labdanes	....	Payne unpublished
D. microzyga F. Muell.	*ent*-labdanes	....	Jefferies *et al.* 1974a
D. attenuata A. Cunn.	*ent*-clerodanes	....	Ghisalberti *et al.* 1973b
D. attenuata A. Cunn. var. *linearis* Benth.	*ent*- clerodanes, lupanes	5,7-dihydroxy-3,6,4′-trimethoxy-	Payne and Jefferies 1973
D. boroniaefolia G. Don.	*ent*-clerodanes,	5-hydroxy-3,6,7,4′-tetramethoxy-	Jefferies *et al.* 1973
BORAGINACEAE—			
Halgania lavandulacea Endl.	....	5,4′-dihydroxy-7-methoxy- 5,7-dihydroxy-4′-methoxy- 5,7-dihydroxy-3,4-dimethoxy- 5-hydroxy-3,4′,7-trimethoxy-	Stacey 1970
DICRASTYLIDACEAE—			
Cyanostegia angustifolia Turcz.	*ent*-clerodanes	5,4′-dihydroxy-3,7,8-trimethoxy- 5,7,4′-trihydroxy-3,8-dimethoxy- 5,7,4′-trihydroxy-3,8,3′-trimethoxy-	Ghisalberti *et al.* 1967 Jefferies *et al.* 1973
C. microphylla S. Moore	....	5,4′-dihydroxy-3,6,7-trimethoxy- 5,3′,4′-trihydroxy-3,6,7-trimethoxy-	Ghisalberti *et al.* 1967
Newcastelia viscida E. Pritzel	ursolic and betulic acids isopimaradienediol (*21*)	5,4′-dihydroxy-3,6,7-trimethoxy-	Jefferies and Ratajczak 1973
Pityrodia lepidota (F. Muell.) E. Pritzel	clerodanes	....	Ghisalberti *et al.* 1978b
MYOPORACEAE—			
Eremophila alternifolia R.Br.	....	5,7-dihydroxy-3-methoxy- 3,5,7-trihydroxy flavanone	Jefferies *et al.* 1962
E. clarkei F. Muell. R.Br.	cembranes	....	Coates *et al.* 1977 Maslen *et al.* 1977a
E. decipiens Ostf.	decipianes	....	Ghisalberti *et al.* 1975 Maslen *et al.* 1976
E. drummondii F. Muell.	serrulatanes	....	Croft 1977
E. fraseri F. Muell. (var.)	eremanes (cembranes)	5,3′5′-trihydroxy-3,6,7,4′-tetramethoxy-	Jefferies *et al.* 1962 Oh and Maslen 1968
E. georgei Diels (var.)	cembranes (eremane, prezizaenes)	....	Ghisalberti *et al.* 1976, 1977b, Carrol *et al.* 1976, Maslen *et al.* 1977b
E. glabra R.Br. Ostf.	....	(lirioresinol-B dimethyl ether)	Jefferies *et al.* 1961
E. longifolia F. Muell.	....	(safrole, eugenol methyl ether)	Della and Jefferies 1961
E. oppositifolia R.Br.	fatty acids	....	Jefferies and Knox 1961
E. ramosissima C.A. Gardn.	....	5,7-dihydroxy-3-methoxy- 3,5,7,-trihydroxyflavanone	Jefferies *et al.* 1962
E. serrulata (A. Cunn.) Druce	serrulatanes	....	Croft *et al.* 1977
Myoporum beckeri F. Muell.	fatty acids	5,3′,4′-trihydroxy-7-methoxy-flavanone	Goh 1968
GOODENIACEAE—			
Goodenia strophiolata F. Muell.	kaurenediol (*31*)	5,7,3′4′-tetrahydroxy-3-methoxy-	Middleton and Jefferies 1968
G. ramellii F. Muell.	kaurenediol (*31*), labdane	....	Coates *et al.* 1968
ASTERACEAE—			
Olearia muelleri (Sond.) Benth.	*ent*-clerodanes	5,7,3′-trihydroxy-3,6,4′-trimethoxy- 5,7,3′4′-tetrahydroxy-3,7-dimethoxy-	Jefferies *et al.* 1974b
Helipterum craspedoides W. V. Fitzg.	beyeren-19-ol (*27*)	....	Dennison and Mirrington 1975

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The prehistoric environment in Western Australia

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Abstract

Knowledge of various aspects of the local environment, excluding climate (see Wyrwoll, this volume) is reviewed for an arbitrarily chosen period of 200 000 years. Such knowledge is extensive, though patchy, and this combined with the need to fit it into the extensively but patchily understood world scene puts comprehensive reviewing bevond the range of one man. Consequently the review attempts merely to indicate the scope of studies of some aspects of the environment, any one of which might now be reviewed comprehensively with advantage. An attempt is made to review prehistoric mammals comprehensively, and some new information is reported.

So far as present knowledge extends, it is concluded that direct and indirect effects of glacioeustatic changes in sea level, and changes in the mammal fauna would provide the most noticeable contrasts with historic time. For most macroscopic forms of life expansions and contractions of range of familiar species have been characteristic of the prehistoric period rather than changes in form or size. For mammals (and probably for other less well-known groups) extinction without replacement was also characteristic, at times and for reasons which remain obscure, though human influence is suspected. Some changes in range appear to have been vegetationally and hence probably climatically induced, and one or two might be due to interspecific reaction.

Introduction

This review of the prehistoric environment, other than climate (reviewed by Wyrwoll, this volume), is made from the point of view of a human observer travelling backward in time and noting (by simple use of his senses) differences from the environment of his temporal starting point. For convenience, this is taken to be the environment as the first European settlers saw it, not as is seen at the time of writing after 150 years of drastic modification.

This hypothetical journey through time is conceived from the results of technologically-sophisticated investigation, of which there has been a great deal, so that a complete review might become merely an annotated list of studies of late Quaternary phenomena, not only in Western Australia itself, but elsewhere as they affect this large region. To avoid this and so produce a readable short review, I have perhaps fallen into the trap of being altogether too sketchy and selective. But except in the section on prehistoric mammals, there is no attempt to be comprehensive, merely to draw attention to kinds of studies, any of which might be reviewed comprehensively with advantage.

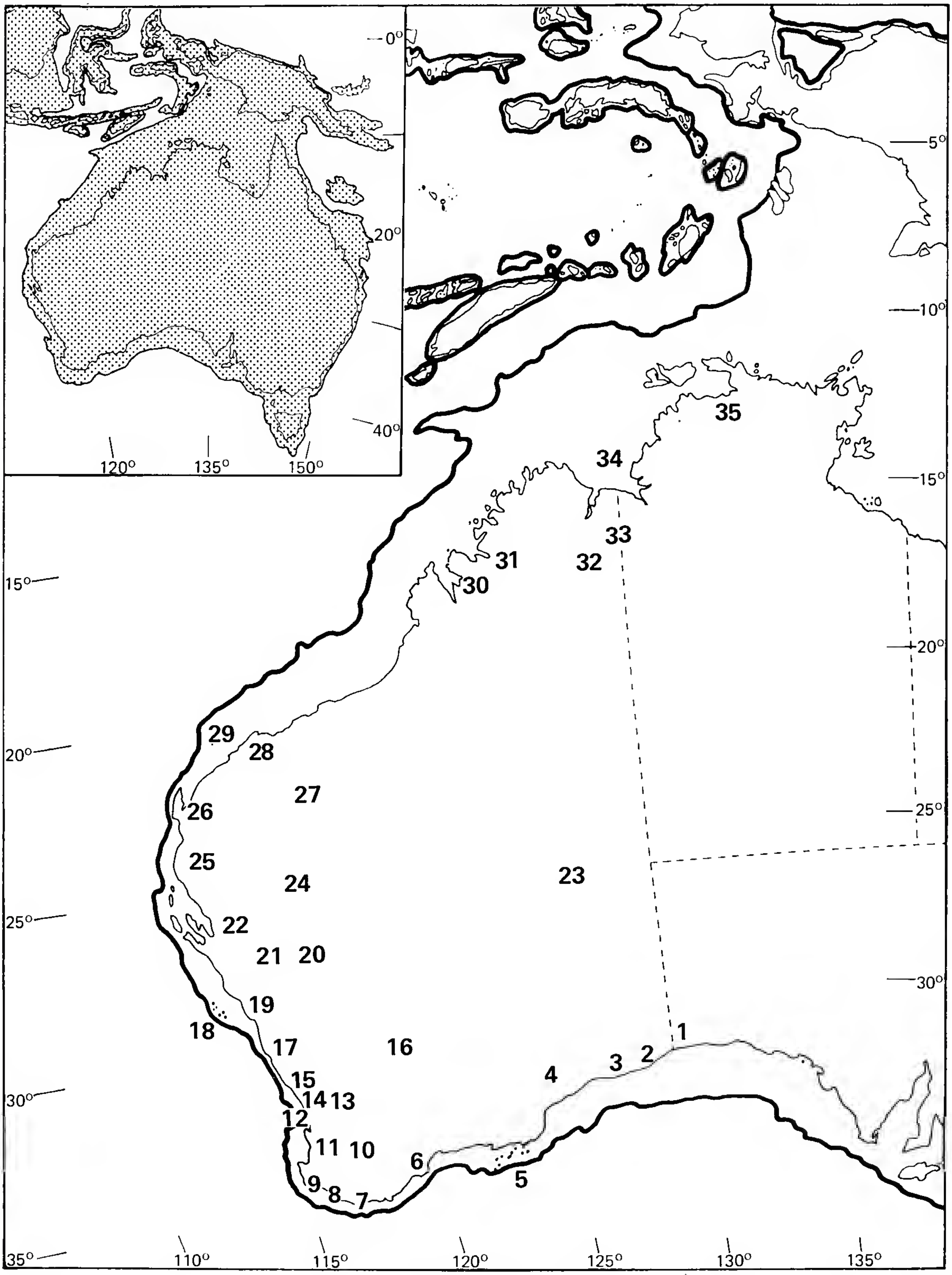
The "prehistoric period" is here taken to begin with the first arrival of hominids in what is now called "Western Australia", which may well be their first arrival in any part of Australasia. This time cannot yet be fixed with any confidence, and so it is necessary to choose a starting point arbitrarily. I choose 200 000 years, knowing that this will seem far too early to many readers and that it is in excess of the estimate of Bowler (in Kirk and Thorne 1976) but finding it convenient and believing it to be reasonable, if not, indeed, too late.

A number in brackets in the text after a locality name means that the locality is indicated in Figure 1. Specimen numbers are those of the Western Australian Museum collections.

Chronological framework

Many phenomena have been shown to have similar periodicity, some no doubt because they are causally related. But whether there were many episodes of about the same amplitude, or a few of large amplitude with many minor oscillations, as implied in the traditional Alpine ice age terminology, is still debatable—e.g. compare Fink and Kukla (1977) with Grootes (1978).

Following Harmon *et al.* (1978b), dealing with Bermuda, I adopt "a picture of long major periods of low sea stand" broken by briefer high level periods, with rapid transition from one to the other (e.g. Broecker and van Donk 1970, Berger *et al.* 1977, Yapp and Epstein 1977). This accords well with studies as diverse as those of Harmon *et al.* (1978a) on North American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speleothems, Luz (1977) on South Pacific planktonic foraminifers or Woillard (1978) on European pollen. Shorn of the obscuring effects of minor oscillations, it is well seen in the study of sea floor sediments off New Zealand by Lewis (1973).

For present purposes I adopt the following synthesis, based mainly on the core near Perth studied by Bé and Duplessy (1976), recognising that there is much controversy about the relative durations of periods of high and low sea level, and about the dates of transitions (the beginning and end dates are arbitrary):

0-10 x 10^3 yr B.P.	Warm, sea initially rising rapidly to level slightly above present, then falling.
10-100 x 10^3 yr B.P.	Cool with low sea levels—minima a little after 70 000 and 20 000 yr B.P., the latter very marked.
100-130 x 10^3 yr B.P.	Warm, high sea levels—maxima a little higher than the present at about 120 000 yr B.P. or a little earlier.
130-190 x 10^3 yr B.P.	Cool, low sea levels—minima about 150 000 yr B.P.
190-200 x 10^3 yr B.P.	Final phases of a warm period—sea level falling rapidly.

Extra-terrestrial events

Many of the climatic effects impinging on prehistoric man no doubt had extra-terrestrial origins, some perhaps resulting from fluctuations in solar output. Sunspot activity may be linked with energy output and hence with terrestrial events, as suggested by Eddy (1976). It is even possible that more distant stars or interstellar material have terrestrial effects, as in the concept reviewed by Dennison and Mansfield (1976), or that of Hunt (1978).

Some effects of immediate terrestrial origin may have interacted with extraterrestrial effects, even if not causally related. For example, there have been several recalculations and much support (e.g. Veeh and Chappell 1970, Emiliani and Shackleton 1974, Weertman 1976, Hays *et al.* 1976, Berger 1977) for concepts of this kind associated particularly with Milankovitch (Kukla 1976). Whyte (1977) has suggested that deceleration of mantle spin velocity is related to reversal of geomagnetic polarity and this in turn to decreasing oceanic ridge activity, marine regression and climatic "deterioration" leading to glaciation. The climatic effects may be due, at least partly, to changes in ionised layers surrounding the Earth with changes in its magnetic field (Cox in Bishop & Miller 1972).

Sun, moon and stars no doubt would have seemed constant throughout our prehistoric period. Differing relative movements related to the precession of the equinoxes might have been noticed by a seafaring people like those of the Pacific islands, but perhaps not by the continental people of Western Australia. But at least one apparently celestial event might have been spectacular, namely the tektite shower, part of it considered by Lovering *et al.* (1972) to have fallen into active seif dunes between 24 000 and 16 000 years ago near Lake Torrens in South Australia.

Horwitz and Hudson (1977) show that the Western Australian tektites covered the whole State, not just the southern part, as formerly believed. They do not suggest a date of fall, but imply this was the same as that of the eastern occurrences, with the possible exception of an apparent indochinite chip from an archaeological excavation at Miriwun (33) in the Ord Valley (Cleverly and Dortch 1975) which may represent a separate fall. There is still an unexplained discrepancy between the isotopically determined age of formation of australites (c. 700 000 yr B.P. or more) and stratigraphically determined ages of fall (late Quaternary, even Holocene) according to Chalmers *et al.* (1976), and until this is resolved, such occurrences as the Murchison River (21) tektite, apparently associated with an extinct marsupial and artifacts (Merrilees 1968c) remain puzzling. Durrani and Khan (1971) suggest that ecological effects might have accompanied the fall of microtektites.

Whether or not prehistoric Western Australians witnessed one or more tektite showers, presumably as a swarm of "shooting stars", the material results of the shower(s) seem to have been a valued component of their environment (Cleverly and Dortch 1975).

Presumably also they witnessed the fall of most or some of the numerous iron and stony meteorites known from many parts of Western Australia, especially the Nullarbor region (compare Wasson 1974), but probably not including crater formation at Dalgaranga (20) and Wolf Creek (32) (McCall 1977). It would be interesting to know if any of these more dramatic occurrences achieved legendary status. Meteorite material, unlike tektite glass, does not appear to have been put to mundane use, but may have had some magical importance.

Figure 1.—Western part of Australasia at minimum sea levels of prehistoric period. Inset: emergent shape of Australasian landmass and proximity to emergent Asia during glacioeustatic minimum sea levels. Numbers represent localities or areas mentioned in the text; 1—Koonalda Cave; 2—Thylacine Hole, Horseshoe Cave; 3—Madura, Murra-el-elevyn and other caves; 4—Balladonia district, Wonberna, Guralla and other rockholes; 5—Archipelago of the Recherche; 6—Bremer Bay district, Reef Beach, Hunter River; 7—Donnelly River, Boggy Lake; 8—Scott River, "Warren Beach"; 9—South-western cave area including Devil's Lair, Mammoth Cave, Skull Cave, Hamelin Bay; 10—Various lunettes; 11—Caves south of Mandurah; 12—Garden and Rottnest Islands; 13—York, Quairading; 14—Mirrabooka, Mosman Park, Leighton Beach, Fremantle, Guildford, Orchestra Shell Cave, Melaleuca Cave, Koala Cave; 15—Gingin district including McIntyre Gully and Caladenia Cave; 16—extinct rivers; 17—Jurien Bay region including Hastings and Weelawadji caves; 18—Abrolhos Islands; 19—Greenough River, Merkanooka; 20—Dalgaranga meteorite crater, Wilgia Mia; 21—Murchison River sites including Billabalong; 22—Shark Bay region; 23—Warburton region including Puntutjarpa rock shelter; 24—Gascoyne River; 25—Lake McLeod; 26—North West Cape region including Monajee Cave; 27—Pilbara rock art sites; 28—Cossack district; 29—Barrow Island; 30—Fitzroy River Estuary; 31—Windjana Gorge, Tunnel Creek; 32—Wolf Creek meteorite crater; 33—Ord River region including Miriwun rock shelter; 34—Joseph Bonaparte Gulf; 35—Alligator River rock art sites.

Volcanic and tectonic activity

Unlike western Victoria (Gill 1972) or the Carpentarian coast (Grimes and Doutch 1978) for example, Western Australia does not appear to have experienced any volcanic activity in the prehistoric period, although of course, indirect effects of volcanicity elsewhere may have been felt climatically (compare Ninkovich and Donn 1976, Bray 1977).

Tectonic activity in this State appears to have been on a much smaller scale than that in the New Hebrides (Neef and Veeh 1977), for example. No doubt earthquakes occurred in the prehistoric as in the historic period, and may be recorded in legend (Hallam 1975), but no geological traces of them seem to have been recorded. Slower movements persisting into prehistoric, perhaps even into Holocene time, have been reported or suggested by Cope (1975), Playford and Cockbain (in Walter 1976), Playford (in Playford and Leech 1977), Denman and van de Graaff (1977) indicating a need for caution in interpreting glacioeustatic markers round the coast (van de Graaff 1978). As with volcanism, it is possible that distant tectonism had effects here (compare Roosen *et al.* 1976).

Coasts and islands

Glacioeustatic low sea levels probably would produce coastal changes noticeable by our hypothetical time traveller, particularly where he had some stable and familiar marker of position, such as the Darling Scarp provides along the south-western coast. Since the present is a time of glacioeustatic high sea level, with only two comparable levels in the last 200 000 years, the effects of these probably would be scarcely noticeable (cf. Tankard 1975, Marshall and Thom 1976, Smart 1977).

The approximate coastline of the minimum prehistoric sea level (c. 17 000 yr B.P.) is plotted in Figure 1 on the assumption that the blanket of sediment deposited subsequently has not altered the once emergent landscape to any great extent, and that glacioeustatic movements are of about the order of magnitude reported by Chappell and Thom (in Allen *et al.* 1977).

The great extension of the northern Australian lowlands during times of low sea level is noteworthy, and effects on prehistoric human populations and on climate would be profound. The lesser extension of the south-western and southern coasts might still have affected local people appreciably, as in the case of Devil's Lair (Balme *et al.* 1978).

All islands (and reefs) at present within about 150 km from the Western Australian coast would have been parts of the mainland at least twice, more likely three times, within our arbitrary "prehistoric" period, and twice or three times isolated, including the present high sea level period of isolation.

Incorporation with the mainland and isolation of islands have been discussed, in several cases in the context of effects on animal and plant populations, in the specific cases of Barrow Island (29) (Main and Yadav 1971), the shore near Lake McLeod (25) (Denman and van de Graaff 1977), Bernier, Dorre and Dirk Hartog Islands (west of 22) (Kendrick 1978), the Abrolhos (18) Teichert 1947, Storr 1965), Garden and Rottnest Islands (12) (Churchill 1959, Playford and Leech 1977) and the Recherche Archipelago (5) (Fairbridge and Serventy 1954, Main 1961). Only the most recent of these studies have been able to take tectonic as well as glacioeustatic movements into account.

Submarine canyons off the present southern Australian coast are discussed by von der Borch (1967). Most of the major ones seem to have been cut long before our prehistoric period, and presumably would have been established and noteworthy features of low sea level coasts during this prehistoric period. A brief review of southern continental areas now submerged is given by Playford *et al.* (1976).

Rivers, lakes and springs

Most of the sporadically flowing or extinct rivers and dry lake beds often given undue prominence in maps of Western Australia seem to have had their genesis at least as early as the Cretaceous, and to have ceased to carry water by the Miocene (van de Graaff *et al.* 1977) except temporarily. Thus they had assumed their present aspect long before our prehistoric period began, and in this long perspective, prehistoric fluctuations probably were minor. Nevertheless, such fluctuations might have been important to the prehistoric people.

For example, Kendrick (1977) shows that the Swan estuary supported an essentially marine fauna at least as far upstream as Guildford (14) in mid-Holocene time. The regional aridity implied by this no doubt had far reaching human effects, and one immediate effect would have been on the quality and quantity of food available to river bank dwellers. Not until some time after 4 500 B.P. was the existing hydrologic seasonality of the river established (or re-established).

An apparent association of prehistoric man and the large extinct marsupial *Zygomaturus* in the middle reaches of the Murchison River (21), reported by Merrilees (1968c), has been investigated recently by Clarke and Lofgren, who suggest (pers. comm.) that the association is real and that it dates from a time of higher river discharge than the present, possibly from a declining phase of the previous major interglacial, of the order of 100 000 years ago. A new discovery of the same association has been made in the Greenough River (19) (Dortch and Wyrwoll, in press), with a suggested age in excess of 40 000 years. It is conceivable that the presence of the large herbivore and the high river discharge had a causal climatic connection of great importance to the people concerned. (It is possible also that the occurrences of what appears or is reported to be *Diprotodon* at Karonie, Lake Darlot, the Great Victoria Desert and the Oakover River (Merrilees 1968c) date from lake- or river- full episodes within our prehistoric period, though there is no indication at present of any association with artifacts.)

A review of drainage patterns over the whole of Western Australia, involving reconstruction of ancient systems now ill defined, is given by Mulcahy and Bettenay (1972), who recognize six major divisions (see also van de Graaff *et al.* 1977). Their South-West Drainage Division is described in more detail by Bettenay and Mulcahy (1972). If rivers in the usual sense did exist during our prehistoric period in the now arid or semiarid interior, they would have been in the positions shown by these authors, but they do not attempt to date river- (and lake-) full periods.

According to Bowler (1976), many Western Australian lake beds may have held water during the prehistoric period, but it is likely to have been saline. Many have been dry long enough for elaborate human use, e.g. the stone arrangements on Lake Moore (16) (Gould and Gould 1968).

Modern groundwater phenomena have been extensively examined in some areas, but not often dated. However, the subsurface structures in the Mirrabooka area (14) north-east of Perth (Allen 1977), for example, which determined the sites of modern springs and soaks presumably has changed only at the most superficial level since the prehistoric period began, and the springs and soaks concerned, though varying in volume as effective precipitation varied (Wyrwoll, this volume), might have persisted through this period. Similarly, if the Bassendean Dune System is indeed earlier than "prehistoric", as McArthur and Bettenay (1960) suggest, then the interdunal lakes, swamps and seasonal streams which are very prominent on these dunes over most of the Swan Coastal Plain might also have persisted. But presumably the terrestrial water table responded to glacioeustatic sea level movements in ways not at present clear, and our understanding of ground-water effects is further clouded by large scale destruction of the natural plant cover for agricultural and other purposes and by the relationship of present ground water to past aridities (Kendrick 1976).

Rocks, landforms, soils

Australia separated from the rest of Gondwanaland, the Indian Ocean came into being, and the basic geological structures which determine landforms were in existence long before our prehistoric period, as succinctly outlined in Geological Survey of Western Australia (1975) and, with special reference to the south-west, by Playford *et al.* (1976). Against such a background, prehistoric changes could only have been on a minor scale.

Differences from the present most easily recognised by a time traveller probably would be those associated with glacioeustatic low sea levels. Thus Clarke and Dortch (1977) present an early Holocene view of their Minim Cove (Mosman Park) locality as perched on a high limestone ridge overlooking the deep gorge of the Swan River (14), presumably in transition from even more extreme dissection a few thousand years earlier, with a coast about 50 km away, to its present state of low relief, broad estuary and coast within 2 km.

Another noticeable by-product of glacioeustatic movements, including those of prehistoric as well as earlier Quaternary time would be the aeolianites of the Tamala Limestone. A long series of studies on similar aeolianites on Bermuda, summarized by Harmon *et al.* (1978b) has tended to confirm early concepts of the source material having been produced in the warmed seas of interglacial times, to be transported landward in times of retreating seas, and lithified during times of low sea level. If so, we must envisage at least three dune generations within our prehistoric period, and such dunes are likely to have transformed the local landscape. Studies of a small area near Fremantle (14) (Kendrick, in prep.) are likely to test the local applicability of these Bermudan concepts; these studies hinge on the interpretation of the two late Pleistocene radiocarbon dates mentioned by Playford *et al.* (1976).

The importance of caves and cave deposits is so great to the prehistorian (Bowdler 1975) as to tempt him to overestimate the importance of caves to prehistoric people. Yet these people clearly did use caves, not only shallow rock shelters such as Miriwun (33) (Dortch in Wright 1977), but also deep limestone caves. Perhaps the most dramatic case is that of Koonalda Cave (1), just outside Western Australia (Wright 1971), but Balme *et al.* (1978) and Clarke *et al.* (in press) show that the present small extent of Devil's Lair (9) is misleading about its depth when it was in prehistoric human use. It may be that the midden locations in Mammoth Cave (9) (Archer *et al.* in press) were deeper within the cave when they were in use than they are now, through downstream migration of the entrance. Many other caves were used by prehistoric groups, some apparently for domestic purposes, others (e.g. Orchestra Shell Cave (14), Hallam 1974) perhaps for ritual use.

Caves are very numerous in Western Australia now, and presumably were throughout the prehistoric period. Descriptions are far too numerous to cite here, but lists with brief individual notes and full references are given for various regions, notably the Augusta to Calgardup Brook district (9) by Bridge (1973) and Bridge and Shoosmith (1975), for the Yallingup area by Bridge (1972), for the Moore River to Jurien Bay (17) by Shoosmith (1973) and Bridge (1973) and for Cape Range (26) by Shoosmith (1977). Nullarbor caves are listed by Dunkley and Wigley (1967), with some emendations by Lowry and Jennings (1974). There appears to be no review or list of Kimberley caves, but Jennings and Sweeting (1963, 1966) and Lowry (1967) describe large caves and briefly mention others.

Karst phenomena other than caves are also common in Western Australia, for example the depressions now occupied by salt lakes on Rottnest Island (12) (Playford and Leech 1977) and circular depressions on reef flats off the Abrolhos Islands (18) (Playford *et al.* 1976), interpreted as glacioeustatic low sea level products.

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Dominant modern soils, usually correlated with landforms, have been mapped for the whole continent in an "Atlas of Australian Soils" published by CSIRO in association with Melbourne University, with a series of explanatory notes for the various regions (e.g. Northcote *et al.* 1967 for the south-west). Each of the series has an extensive reference list. Presumably the soils now present in most places have taken a long time to develop, and many may be prehistoric in origin, but in general there is little information available on the ages of soils. However, ancient soil structures or soil remnants feature prominently in the Western Australian landscape, for example the pedogenic carbonate, distinguished (as "kankar") from valley fill "calcrete" by Sanders (1974), which is very widespread in the dry interior. This may well be much older than our "prehistoric period".

Buried soils occur in the Tamala Limestone, for example those at Hamelin Bay (9) described by Fairbridge and Teichert (1953). They are often well defined, sometimes well lithified, and may be prominent features of cliffs, or form the roofs of caves, but even so represent short-term highly localized episodes of soil formation in many cases, often in interdunal swales (Clarke *et al.*, in press). There are additionally very densely lithified bands often with solution pipes descending from them, sharply demarcated from overlying non-calcareous sands. Whether these lithified bands ("cap rock" or "capstone" in local lay usage) are horizons in a soil profile including the overlying sand, or are completely separate (as in the site described by Clarke and Dortch 1977) is not always clear. Solution of local problems such as this would seem to be amenable to closer study, and there is a prospect of working out a dune and soil sequence, as has been done in Bermuda (Harmon *et al.* 1978b), which with marine intercalations will permit stratigraphic subdivision of the Tamala Limestone. In the meantime, it is not clear which parts, if any, are "prehistoric" in our sense.

Relative soil and landform chronologies have been put forward for some regions (e.g. for York-Quairading (13) by Mulcahy and Hingston 1961), and an attempt made to establish an absolute chronology for the Swan Coastal Plain by McArthur and Bettenay (1960). Though subsequent refinements in the world Quaternary chronology on which this is based may suggest some revision, it is likely that many of these Swan Coastal Plain soil systems can still be regarded as "prehistoric" in origin.

South-western soils are reviewed by Mulcahy (1973).

Deserts and dunes

With his convenient though European-oriented definition of "desert" Beard (1969) points out that about two fifths of Western Australia is involved and suggests natural divisions. These would seem to have been in existence long before our prehistoric period began, but nevertheless in their extreme form may be Quatenary phenomena, by analogy with the eastern Australian occurrences discussed by Jessup and Norris (1971), Bowler (1976) and others.

If so, the perspective is shorter than for rivers and lakes, and one might expect prehistoric fluctuations in deserts to have had profound effects on prehistoric human populations involved with them. Even now, most desert and desert-fringe dwellers not only in Australia but elsewhere seem to be more at the mercy of this than of most environments, and yet to influence it more profoundly by their mere existence, usually to accentuate if not actually produce desertification (Hare 1977).

By analogy with other parts of Australia (e.g. western New South Wales, Wasson 1976), it would seem that some desert dunes and even sand sheets of modest size might still have been mobile almost to the end of our prehistoric period, and Jennings (1975) and Bowler (1976) demonstrate dune building on a large scale in late Pleistocene time.

One special kind of desert or semidesert landform, the lakeside lunette, seems to have had considerable importance for prehistoric people. Investigations of lunettes in the Murray-lower Darling River region are described by Bowler (1970, in Mulvaney and Golson 1971, 1976), Merrilees (1973a), Marshall (1973), Allen (1974) and others. They have received less attention so far in Western Australia, and may have been less important prehistorically, but some aspects are discussed by Bettenay (1962) and Bowler (1976) (10).

The Western Australian deserts were not empty of people for the whole prehistoric period. Gould (1968, 1977) demonstrates occupation dating back about 10 000 yr., continuing into the historic period. But it is possible that our deserts were only habitable during interglacials, if Gould's stress on the difficulties they now present is in proper perspective.

Air and sea

There is reason to think that the present chemical composition of the Earth's sea and air envelopes is the current stage in a long sequence of evolutionary changes (e.g. Fairbridge in Chilingar *et al.* 1967), but that there has been no catastrophic change in late Cainozoic time. McLean (1978) suggests that land plants have been the major regulators of carbon dioxide and oxygen in the air throughout the Cainozoic, and that the effect of major marine transgressions would be to increase carbon dioxide and concomitantly decrease oxygen content of the air by replacing large areas of terrestrial with marine floras. Possibly reinforcing this effect is another described by Berger *et al.* (1977), a release into the air of carbon dioxide previously trapped in deep ocean water under a "lid" of glacial meltwater at the time when vertical mixing became more effective as deglaciation (and hence marine transgression) proceeded. In view of the importrole of the relatively small quantities of carbon dioxide now present in the air (Bray 1977), it is very likely that prehistoric people would have been affected indirectly by this change two or three times during the prehistoric period.

Fluctuations in the rate of removal of calcium from sea water by plants and animals presumably occur in response to the relatively small

temperature increases (Bé and Duplessy 1976, Shackleton and Opdyke 1977) of interglacial times, as implied or stated in various adaptations of the Sayles model of dune limestone formation (e.g. Sayles 1931). But perhaps they are oalanced by inverse fluctuations in delivery of calcium to sea water by river discharge. On the other hand, if chlorine and bromine are continually discharged into sea, air and sediments (with the sea accounting for a large proportion of this "surface reservoir") by volcanic processes (Schilling *et al.* 1978), then the quantities present will have altered over the prehistoric period. But the rate of alteration presumably would be perceptible only by sophisticated means.

Fluctuations in particulate matter, both in sea and air, might be directly observable. Thus the air of glacial time might have been perceptibly dustier than in historic time (compare Kolla and Biscaye 1977), and smokier in late than in early prehistoric time (Hallam in Wright 1977). A significant and environmentally informative component of dust, not yet studied in Western Australia, is phytoliths (Baker 1959a, b, Smith *et al.* 1970, Rovner 1971). There is still controversy about the sediment load of rivers of glacial compared with interglacial time (Flint 1971, Verstappen 1974), but there might well have been differences, affecting among other easily observable things, the colour as well as the turbidity of the sea, and the distribution of molluscs and other organisms important in prehistoric human diet.

Physical processes in the air of the kind usually summed up as climatic fluctuations are discussed by Wyrwoll (this volume). Similar processes in the more viscous material of the sea might be expected to be slower, but to have no less profound effects, not least through their influence on atmospheric processes (e.g. Berger *et al.* 1977). Wyrwoll (this volume) suggests that surface currents have been significant determinants of climate in Western Australia.

Animals

Mammals

The most recent review of Quaternary mammals in Western Australia is that of Merrilees (1968c), which was not intended to be confined to the "prehistoric period" as defined here, but which in fact largely was so confined. By adding the following notes of new discoveries and studies, an up to date review is obtained.

Rock paintings and carvings, and traditions.—Representations of thylacines have been noted by Wright (27) (1968, 1972), Brandl (35) (1972, 1973) and Lewis (1977), and of devils by McCarthy (1976) and Calaby and Lewis (1977), though many of these are outside Western Australia. These and earlier records of extinct forms, coupled with renewed interest in and appreciation of Aboriginal art (Edwards and Ucko 1973, Ucko 1977, Clegg 1978), might be expected to lead to systematic search for representations of totally or locally extinct taxa, comparable with those of other countries (e.g. Bruemmer 1974, Powers and Stringer 1975).

An oral tradition which might relate to the thylacine (Kolig 1973) exemplifies another avenue of investigation of the prehistoric fauna and the use of *Sthenurus* and *Zygomaturus* teeth in charms (Akerman 1973) still another. The latter occurrence does not necessarily imply coexistence of man with *Sthenurus* and *Zygomaturus*, as interest in and use of fossils by Aborigines seems to have been widespread (Whitehouse 1948, Gill 1957), as by other prehistoric people (e.g. Oakley in Brothwell and Higgs 1969, Kraft and Thomas 1976). Even now, Aboriginal people maintain this interest (M. Lofgren, pers. comm.).

Fossil deposits in the South-West.—Knowledge of these has been extended greatly since the review by Merrilees (1968c), and a new interpretation of the Mammoth Cave (9) deposit put forward by Archer *et. al.* (in press).

Mammoth Cave now has a walk-in entrance, and probably has had for most or all of the period under study, though perhaps not always in its present position. As with most caves in the region, there is a surface scatter of bones, predominantly of mammals with several local concentrations. But there are (or were) also two patches rich in bone buried in partly lithified deposits capped by thick flowstones. These were dug out in the early years of the present century leaving only small remnants, and some of the bone was described from a taxonomic viewpoint, with little attention to provenance, in a series of papers by L. Glauert (see Glauert 1926, under "Pleistocene"). Glauert's findings have been quoted frequently (e.g. by Tedford 1967), but require extensive revision. Some was made by Merrilees (1968c) and some further revision is incorporated in Table 1. Merrilees and Porter (in press) illustrate and give diagnostic characters of some Mammoth Cave fossil material, and tentative reconstructions of some taxa are included in Figure 2.

The two richly fossiliferous patches in Mammoth Cave have been distinguished as the "Le Souef" and "Glauert" deposits respectively by Archer *et. al.* (in press), but material from them was not kept separate by the excavator, and little can be distinguished now. Though separated topographically by about 10 m, the two deposits appears to be strategically continuous. Several layers can be distinguished in the remnant of the "Glauert deposit" and at least two in the "Le Souef deposit", but material from these layers was not labelled separately, and only some specimens can be distinguished with confidence as from one or other layer. The lowest layer, probably the one containing all or most of the extinct taxa, has an age beyond the present practical range of radiocarbon dating (>37 000 radiocarbon yr B.P.; Merrilees 1968c).

As a result of studies of a variety of marks on the bones, Archer *et. al.* (in press) conclude that a notch on a fragment of *Sthenurus* tibia is man made, and conclude also that extensive breakages of large limb bones are artificial. Some of the bone is charred and two fragments possibly represent human skull, but no stone tools have been detected so far. From this

Table 1

Revised list of vertebrate remains from Pleistocene deposits in Mammoth Cave, i.e. from "Glauert" and "Le Souef" deposits (Archer et al. *in press), ignoring undated material from elsewhere in the cave.*

Monotremes	
Tachyglossus aculeatus	e.g. 61.7.14
Zaglossus hacketti (= *Z. bruijini?*)	e.g. 60.10.1
Echidna of intermediate size	e.g. 61.6.6
Carnivorous marsupials of medium or small size	
Dasyurus geoffroyi	e.g. 66.9.10
Phascogale tapoatafa	e.g. 66.9.7
Antechinus flavipes	e.g. 68.6.285
Sminthopsis murina	e.g. 68.6.286
Sarcophilus harrisii	e.g. 66.9.14
Thylacinus cynocephalus	e.g. 61.2.25
Bandicoots	
Isoodon obesulus	e.g. 66.2.195
Perameles (P. bougainville?)	e.g. 66.7.12
Possums, koala, wombat, etc.	
Trichosurus vulpecula	e.g. 70.3.27
Pseudocheirus peregrinus	e.g. 69.3.767
Thylacoleo (T. carnifex?)	e.g. 64.10.25
Phascolarctos (probably *P. cinereus*)	e.g. 64.2.26
Vombatus hacketti	e.g. 65.1.21
Macropods	
Potorous tridactylus	e.g. 66.3.65
Onychogalea (possibly *O. unguifera*)	e.g. 69.3.831
Macropus eugenii	e.g. 69.3.637
Macropus irma	e.g. 66.9.36
**Macropus fuliginosus*	e.g. 69.2.241
Setonix brachyurus	e.g. 69.3.219
"Mammoth Cave wallaby"—an unidentified, probably undescribed species about the size of *Wallabia bicolor* or *Macropus agilis*, represented by juvenile dentaries, e.g. 66.8.17. Adult maxillary fragments (e.g. 66.8.18) may or may not represent the same species	
Sthenurus brownei	e.g. 63.2.198
Sthenurus occidentalis	e.g. 62.8.31
Protemnodon brehus	e.g. 64.2.18
(?*Protemnodon* larger than *P. brehus*	—e.g. 65.4.153)
Diprotodontid	
Zygomaturus trilobus	e.g. 61.8.3
Eutherians	
Bat	e.g. 71.3.64
(?*Pseudomys albocinereus*	e.g. 76.2.92)
Pseudomys shortridgei	e.g. 76.2.94
Rattus fuscipes	e.g. 72.4.1
Birds	
Small species	e.g. 67.7.1
Eagle-like species	e.g. 61.6.12
Emu-like species	e.g. 65.4.152
Reptiles	
Wonambi naracoortensis	e.g. 68.4.30
Lizard	e.g. 76.2.86
Amphibians	
(?Frog	e.g. 76.2.96)

* A second species similar in size to *M. fuliginosus* is reported by Merrilees (1968c). No detailed statistical analysis has been made, but it now seems likely that all the large macropodine cranial material could be included under *M. fuliginosus*. The possibility that *M. giganteus* might be present has not been investigated.

evidence and from the position of the material on top of large blocks of limestone fallen from the roof of the cave, Archer *et al.* suggests that man was the main bone accumulator in this case.

Bone in the Devil's Lair deposit also appears to be the leavings of predators, mainly man in the upper layers and owls in the lower, with an intermediate zone of overlap. Analysis of this bone, representing uninterrupted but slow accumulation over the period approximately from 35 000 to 5 000 yr B.P., has been made by Balme *et al.* (1978). They report fluctuations in the relative proportions of 23 mammal species, and sporadic presence of another 11. For present purposes, the most noteworthy of these fluctuations appears to be marked decline in latest Pleistocene and early Holocene time of a group designated as "non forest" mammals (*Perameles, Bettongia lesueur, Petrogale, Pseudomys albocinereus, P. shortridgei* and *Notomys*) with concomitant increase in *Potorous* and *Setonix*.

Remains of extinct mammals (e.g. *Sthenurus brownei*) represented at Mammoth Cave, and of others like *Phascolarctos*, which vanished from the region before historic time, are present in the lower layers in Devil's Lair (9), but it seems likely that these are secondarily derived from another deposit of unknown age, beyond the usual range of radiocarbon dating (Balme 1978).

Porter (1979) describes a deposit in Skull Cave (9), spanning all or most of the Holocene, with bones apparently representing animals which fell into what was essentially a large pit, could not escape, and so died. But there may have been a contribution from owls. All the mammal taxa present were still extant in historic time, though not all were present in the district. There are undated deposits elsewhere in Skull Cave which on field evidence seem to be older than that described by Porter (1979), and *Zygomaturus* is represented in these (R. Howlett, pers. comm.); they are still under investigation.

Small cavities in cliffs at Deepdene, which seem to have served as owl roosts, are described by Archer and Baynes (1973). Mammal remains in these represent the small mammal fauna of the region only a few hundred years before the early historic period.

Occurrences of *Petrogale* in south-western cave deposits have been described by Merrilees (1979), and new discoveries of extinct taxa have been made in The Labyrinth (Merrilees 1969), at Hamelin Bay (*Vombatus*, specimen 77.8.102) and in Crystal Cave (*Protemnodon*, probably *P. brehus*, 78.2.4 and *Sthenurus* sp., 78.2.3.) (All 9).

Coastal dune sites along the south coast have been systematically searched for mammal remains in connection with a determined attempt by the Department of Fisheries and Wildlife to locate living colonies of *Potorous tridactylus*. Large numbers of *Setonix* specimens were collected, with smaller numbers of other extant taxa, not yet reported in detail. Butler (1969) reports mammals (including *Sarcophilus*) from such a dune (8), undated, and Butler and Merrilees (1970) list a fauna including *Potorous platyops* and *Antechinus apicalis* from another dune (6), considered to represent owl prey and to date from about 1 000 yr B.P. Another owl pellet deposit in a small cliff cavity at the mouth of the Donnelly River (7), briefly mentioned by

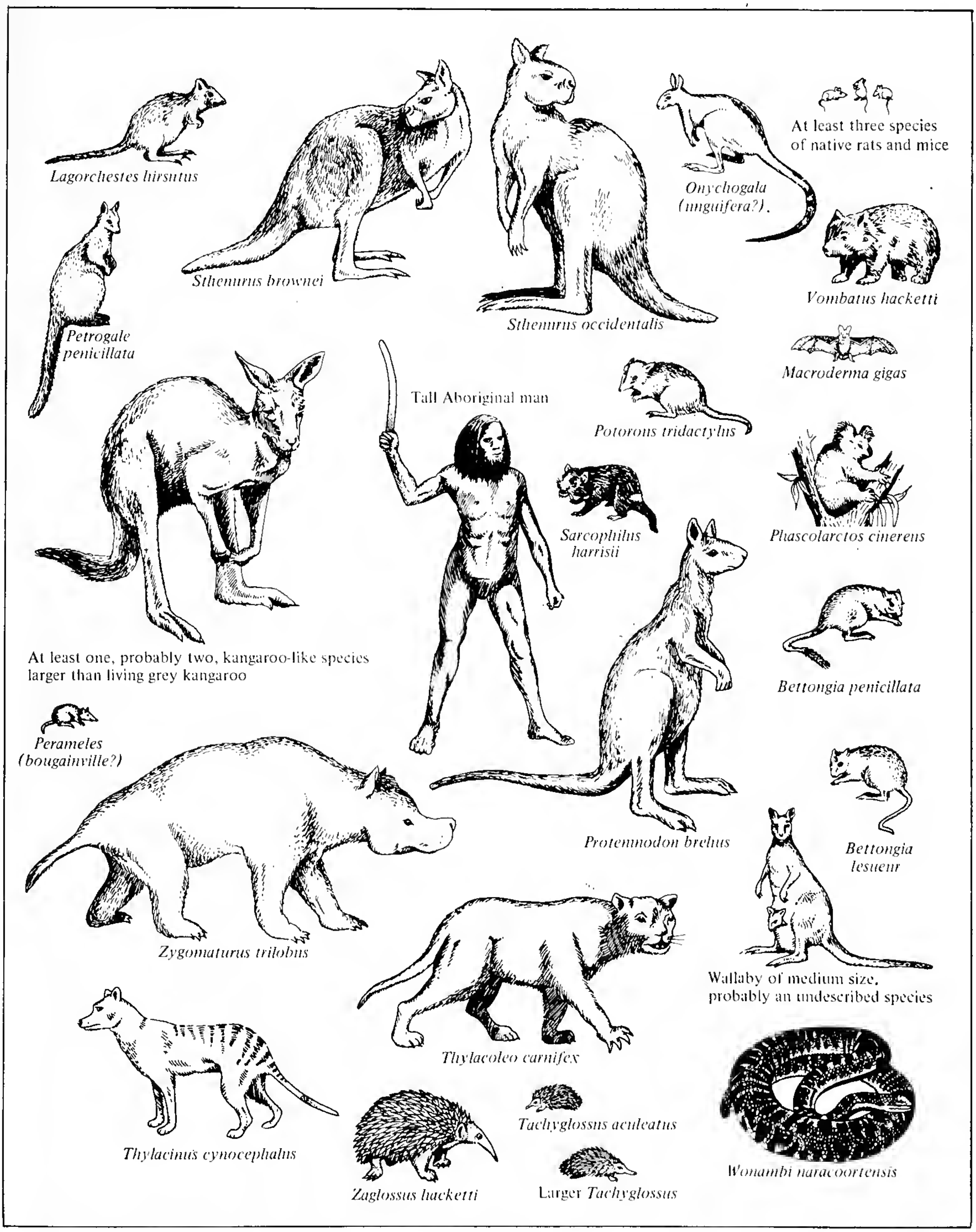

Figure 2.—Some prehistoric inhabitants of the extreme South-West, now extinct there. All to same scale.

Archer and Baynes (1973 p.88), has not been examined in detail. Merrilees (1970b) reports the finding of *Zygomaturus* in dune limestone near Bremer Bay (6); charcoal collected with this specimen has been dated subsequently as greater than 32 000 yr B.P. (GaK - 2542, Kigoshi *et al.* 1973).

Further north, the wheat belt remains virtually blank palaeontologically, and the small caves of the coastal region between Perth and Bunbury have been relatively unproductive, despite systematic search by speleologists. However, *Bettongia lesueur* (76.4.9) has been found near Mandurah (11) presumably of prehistoric age.

In the metropolitan region, there have been new finds of *Protemnodon brehus* (76.3.2) near Leighton Beach (12), and *Sthenurus occidentalis* (76.6.19) at Melaleuca Cave (15), Yanchep National Park, both of unknown age. Archer (1974) describes a late Holocene prehistoric fauna (including *Onychogalea lunata*) from Orchestra Shell Cave (15), Wanneroo and Archer (1973) records what appears to be an older deposit, with remains of *Sthenurus brownei, Potorous platyops, Phascolarctos, Vombatus* and *Perameles* from Koala Cave (15), Yanchep. This may or may not be prehistoric. Amendments to the account by Douglas *et al.* (1966) of a deposit at Wanneroo (15) include the recognition in it of at least one artifact (Merrilees 1973b), and of *Onychogalea* (probably *O. lunata*—65.10.164, 188, 190) among specimens previously misidentified as *Petrogale*.

Further north, excavations in Hastings Cave (17), not yet reported, have shown substantial changes in the mammal fauna during the Holocene, and have confirmed the presence of *Protemnodon brehus* (72.12.173) (A. Baynes, pers. comm.). Excavations in Caladenia (15) and Weelawadji Caves (17) have not yet been reported, and new finds have been made in the Gingin district (15) where Tyrer (1971) reports a *Protemnodon* molar fragment of indeterminate species (69.9.10 is a cast of Tyrer's specimen), and Roe (1971) records a late prehistoric or early historic fauna from a small excavation.

Repeated visits to the *Zygomaturus* locality in McIntyre Gully (15), Gingin (Merrilees 1968c p.13) by R. Roe, F. Dodds and others have produced a series of new finds, including further *Zygomaturus* specimens, one reported by Merrilees (1970b). Specimens from McIntyre Gully not so far reported include a dentary fragment (78.7.2) representing an apparently undescribed species of *Sthenurus* larger than *S. occidentalis*. Post-cranial fragments tentatively ascribed to *Sthenurus, Protemnodon, Macropus* cf. *M. fuliginosus*, and a medium sized macropodine have been recovered, as well as a small number of specimens representing *Macropus irma, Bettongia* (probably *B. penicillata*), *Setonix, Isoodon* and *Dasyurus*. The specimens concerned are 78.7.2-25, 75.12.2 and 69.4.48-52.

The geological character of the McIntyre Gully deposit remains obscure, and material of modern and Cretaceous age is mixed with presumed Pleistocene material, not always readily separated by appearance. There are shallow incisions on at least one fragment of a small limb bone (69.4.50), but no certainty that these are artificial and no other suggestion of human presence.

A *Zygomaturus* mandible (77.9.10), with stone artifacts from the same bed (Dortch and Wyrwoll, in press) was discovered in the bank of the Greenough River (19), in 1977, and a collection of fragmented bone, representing a variety of mammals (including *Leporillus apicalis* and *Onychogalea lunata*) as well as birds and other taxa was made at Merkanooka (19). The latter collection 65.11.22-28, 66.1.6-11, 68.1.30-48 included artifacts and charred bone, but whether of prehistoric or early historic age is not certain.

North-West Division.—Association of artifacts with *Zygomaturus* remains from the Murchison River (21) reported by Merrilees (1968c), has been confirmed (J. D. Clarke and M. Lofgren, (pers. comm.). Burbidge and George (1978) quote finds by A. Baynes and D. Merrilees of "sub-fossil", presumably prehistoric, mammal remains, including *Leporillus conditor* on Dirk Hartog Island (west of 22) and A. Baynes is studying material collected by him in other parts of the Shark Bay region.

Thylacinus and other taxa are reported from cave deposits on North West Cape (26), at least one of which (in Monajee Cave), has an archaeological component (Kendrick and Porter 1974).

Kimberley Division.—Archaeological deposits of Holocene and very late Pleistocene age in the Ord River region (33) are described by Dortch (in Wright 1977). Some of these contain mammal remains, not yet analysed in detail. Archer (1975) lists *Thylacinus* and other mammals from the Tunnel Creek area (31) which might be "prehistoric", if indeed not "historic" in time. Small numbers of specimens of extant taxa from scattered localities are present in the Western Australian Museum collection, and a *Protemnodon* specimen in the Queensland Museum collection is reported to come from the old "Rosewood" station, later part of Argyle Downs (33); these are not dated.

Eastern Division.—This vast area is represented only by very scattered specimens of extant taxa, by the few poorly preserved specimens of *Diprotodon* mentioned by Merrilees (1968c), by a Holocene archaeological sequence at Puntutjarpa (23) containing highly fragmented bones of extant mammal taxa (Archer in Gould 1977), and another at Wilgie Mia (20). The Wilgie Mia collection (73.1.154-253, including *Chaeropus, Leporillus apicalis* and *L. conditor*) is under study by A Baynes.

Eucla Division.—Thylacines are known to have persisted into late Holocene time in the Nullarbor region (2, 3) (Lowry and Merrilees 1969, Merrilees 1970a, Lowry 1972), after the arrival there of dingoes (Archer 1975, Milham and Thompson 1976). (Dingoes also arrived in the Cape Leeuwin-Cape Naturaliste region before thylacines disappeared from it (Merrilees 1979)).

An excavation in Madura Cave (3) with an apparent association of *Protemnodon*, two species of *Sthenurus* and *Phascolarctos* with an otherwise

modern-seeming fauna and artifacts has been reported by Milham and Thompson (1976), but at least the *Protemnodon* and by implication the other archaic taxa have been shown to be secondarily derived. Other faunistic results of a joint University of Sydney-Australian Institute of Aboriginal Studies Nullarbor archaeological survey (which included the Madura Cave excavation) have not been published. However, Archer (1972) independently has listed mammal remains from an excavation in one of the caves examined in this survey, Horseshoe Cave (2) with radiocarbon dates showing it extended back into the Pleistocene.

Pleistocene dates (all on bone) are listed by Lundelius and Turnbull (1973) with an ongoing series of taxonomic studies (e.g. Lundelius and Turnbull 1975) for still other excavations in Madura Cave.

The Western Australian Museum collection contains an abundance of material from Nullarbor caves, not yet studied in detail or reported even at the simple "interesting occurrences" level like that of Merrilees (1968d) for *Chaeropus*.

Lower vertebrates

Peculiarities in the modern geographical distributions of many bird taxa have led to inferences about their prehistoric status. For example, Mayr (1944) concluded that certain species like the nankeen kestrel (*Falco cenchroides*) invaded Australia by way of Timor during some not very remote time of glacioeustatic low sea level, and that because most such species were grassland birds, climatic conditions must then have been much drier than the present. This last logical consequence of Mayr's thesis flatly opposed a strong current of opinion which then equated low latitude "pluvials" with high latitude glacials, a current now largely reversed. Fairbridge (1976) outlines the interesting history of this reversal of opinion, and Van Devender (1977) and Brakenridge (1978) present alternative views on ". . . the American Southwest . . . one of the last areas in the world considered by many to have experienced true glacio-pluvial climates," in the latter's words.

Geologically recent arid periods have been postulated as isolating mechanisms, leading to speciation within the continent, by Serventy (1951) for wrens (and Main *et al.* 1958 for frogs), but pluvials also have been considered to have this function (e.g. Ford 1974). Such postulates usually have been linked with contemporary opinion about the timing of climatic changes, and there has been little study of available fossil bird material which, if reliably dated, might yield direct insight into prehistoric fluctuations in bird distributions.

One fossil occurrence which may or may not be prehistoric is that of a very large, thick-shelled egg found by V. Roberts in a blown-out coastal sand dune south of the Scott River (8), and kindly loaned by the finder to the Western Australian Museum for study and display; it is mentioned briefly by Rich and van Tets (1976). It appears to be an *Aepyornis* egg from Madagascar. Associated material of apparently very mixed origin, typical of blown-out dunes, is described by Butler (1969). This egg might have been a collector's item washed overboard from a passing or wrecked ship, but it is robust, was intact when found and could quite conceivably have floated from Madagascar, as suggested by Lodge (1976), a reasonable suggestion in the light of studies of drifting objects reported by Shannon *et al.* (1973, especially Figure 4). Perhaps its main relevance here is as an example of the arrival of bizarre material from an unknown external environment in prehistoric time, comparable with the tektite shower mentioned above.

Although prehistoric reptilian material is recorded for many Western Australian excavations (e.g. Puntatjarpa (23), Archer in Gould 1977) and is sometimes abundant (e.g. Devil's Lair (9), Balme *et al.* 1978), little study has been made of it. However, the very large boid snake *Wonambi naracoortensis*, initially described from south-eastern South Australia (Smith 1976), is also known from two Western Australian sites, Mammoth Cave (9) and Koala Cave (15), (M. J. Smith, pers. comm.). A tooth from the Gascoyne River district (24) mentioned by Merrilees (1968c p.15) now appears referable to the extinct crocodilian *Pallimnarchus pollens*, and like the possibly crocodilian vertebra from the Ederga River (19) still further south, may or may not be prehistoric. Similarly undated crocodilian and chelonian occurrences in the west Kimberley region (31) are described by Gorter and Nicoll (1978).

Study of frog remains from the extreme south-west (Balme *et al.* 1978, Porter 1978) is in a very early stage, and although fish remains have been reported from some excavations (e.g. Miriwun, 33, in the Ord River region, Dortch in Wright 1977) and some study has been made of them, little information is available.

Invertebrates

In abundance, variety of species and indirect effects on people, prehistoric invertebrates no doubt merit far more extensive study than all vertebrates combined, as in the historic period. Yet for lack of interest perhaps as much as lack of durable remains, there has been very little study of any group other than molluscs. As in the case of birds, some writers (e.g. Richards 1971, Gray 1974) have inferred prehistoric or earlier status from present geographical distributions, but have not had the backing of direct study of fossils.

Late Pliocene and Quaternary molluscs, both marine and otherwise, have been reported by Kendrick (1960, 1973, 1976, 1977, 1978 and in Playford and Leech 1977), and he has work in hand on a sequence of marine faunas from the Perth Basin, some of prehistoric relevance (pers. comm.). In general, the marine molluscs (together with corals and some other taxa) indicate migrations or extinctions in response to temperature changes, the non-marine molluscs in response to aridity, but not all the observed changes can be related to our "prehistoric" period. Extinction of *Bothriembryon douglasi* and *B. ridei* and the appearance of camaenid

snails in the Shark Bay region, however, is attributed to a change from more to less humid conditions perhaps of the order of 80 000 yr B.P. (Kendrick 1978). Occurrence of marine molluscs near Guildford (14) has been taken to indicate a mid-Holocene period of aridity near Perth (Kendrick 1977). Fairbridge (1950) discusses the origin of coral reefs, some prehistoric.

Plants

As noted above for rivers and lakes, so for vegetation the most profound transformation of the Western Australian scene from one of tropical luxuriance to its familiar sparseness took place in the early or middle Tertiary, long before our "prehistoric" period began (Churchill 1973, Wilde and Backhouse 1977, Kemp 1978). But vegetational fluctuations in the prehistoric period, though within this framework of overall sparseness, may still have had far-reaching effects on prehistoric people.

Unfortunately in Western Australia there have been no studies of long pollen sequences comparable with those which have been environmentally so informative in eastern Australia (e.g. Dodson 1977, Colhoun 1978, Kershaw 1978). But shorter sequences have been reported by Churchill (1968) for the extreme south-west (7, 8, 9) and Martin (1973) for the Nullarbor (3). Churchill reports fluctuations with time in the distribution of common eucalypt species thought to be related to fluctuations in rainfall. Martin (and Martin and Peterson in Pittock *et al.* 1978) relates changes in relative abundance particularly of chenopods and eucalypts to changes in sea level.

Still, briefer glimpses of the vegetational past are given by Churchill (1959, 1960 and in Hallam 1974); Storr *et al.* 1959 and Playford and Leech (1977) for a region round Perth, including what is now Rottnest Island (12). Jennings (1975) reports the occurrence in mid-Holocene time of mangroves much larger than any now known, in the Fitzroy estuary (30), apparently related to rainfall changes. Various sites on the south coast, each with Holocene dates, are described by Balme (in Dortch 1975), Bermingham *et al.* (1971) and Butler and Merrilees (1971). Another south coast site (8), not hitherto reported, is "Warren Beach" (an informal name) nearly west of Northcliffe, at which tree stumps, apparently in growth position, can be seen submerged for some hundreds of metres out to sea. An extensive peat bed, possibly the substrate in which the trees grew, seems also to be present. Wood from one of the stumps has been dated at 8 340 ± 135 yr B.P. (SUA-343, R. Gillespie, pers. comm.). Since sea level at this time would have been of the order of 20 m lower that at present and the sea floor shelves gently, the trees concerned might have been as far away from the sea as their present day counterparts are, and there may be no climatic significance in the occurrence. However, detailed studies have not yet been made, nor the possibility of tectonic movement examined (compare Cope 1975).

Parsons (1970) and Nelson (1975) studied disjunct plant distributions in the Nullarbor region and the latter concludes that some represent disruption (presumably during the last major glacioeustatic low sea level) of once continuous distributions. Ingram (1969) reports vegetation like the present in this region (2) in late prehistoric time.

Algal stromatolites, permitted to flourish in the Shark Bay region (22) by an unusual set of circumstances which developed in late prehistoric time, are discussed by Playford and Cockbain (in Walter 1976), and Churchill and Sarjeant (1962) and Harland and Sarjeant (1970) discuss another unusual aquatic plant occurrence, acritarchs in the undoubtedly non-marine environment of a deposit at Boggy Lake (7), on the south coast.

In addition to these more or less direct studies of plant remains, inferences have been made about plants indirectly from studies of animals, e.g. those of Mayr (1944), Balme *et al.* (1978) and Merrilees (1978), previously mentioned.

Apart from the novelties shown by the aquatic plants, all of these cases represent fluctuations in floral composition or migrations of communities on a minor scale compared with the major Tertiary transformation mentioned above.

The impact of man-made fires on vegetation in prehistoric time is reviewed by Hallam (1975) and suggested to have been more profound than generally appreciated.

People

A vital component of a prehistoric person's environment would have been his fellow men. The following review of this component has been made by M. Lofgren:—

"Just how long ago hominids first arrived in what is now called Western Australia is as yet largely a matter for speculation. Already, limited research completed in this vast and diverse area has established radiometrically documented occupational dates (9) (Dortch, in press) comparable to the oldest dates reported elsewhere in the continent (Bowler in Kirk and Thorne 1976). Beyond this generally accepted age of c.40 000 B.P. (Jones 1977) are provocative sites and associated materials currently undatable by existing techniques excepting geomorphological inference. For example, sites along the middle reaches of the Murchison River (21) (Merrilees 1968c) may well be related to the declining phase of the last interglacial, in the order of 100 000 B.P. (Clarke and Lofgren, in preparation). Such an enormous occupational time span potentially involves a far more complex human prehistory of Australia than could have been imagined even a few years ago.

"One aspect of this complexity centres upon the identity of those first migrants to the new Australian world. Indeed, the timing of that first arrival is significant in understanding various aspects of human evolution both outside and within Australia (Howells 1973), eventually leading to those people now called Australian Aborigines. While the irreducible founder population

might have been a young pregnant female accidentally landing on the coast of the new land (Calaby in Kirk and Thorne 1976), a far more likely scenario would envision the purposeful movement of coastally-adapted family groups (Bowdler in Allen *et al.* 1977). Though the failure rate of such movements must have been high, separate landing—some certainly on the coast of Western Australia—over centuries and indeed millenia (for possible routes, see Birdsell in Allen *et al.* 1977) eventually led to the human colonization of the continent.

"Clues as to the biological origins and subsequent evolutionary course of those first migrants may be derived from a variety of sources (e.g. Howells 1973, Kirk and Thorne 1976). Direct evidence from studies of prehistoric human skeletal material, both Pleistocene and Holocene, are vital in this regard. In the past, virtually all these studies were restricted to material derived from a limited area of south-eastern Australia. Now, a recent study (Margetts and Freedman 1977) establishes a vital Western Australian baseline against which other late prehistoric Australian populations may be compared, as well as providing a measure to help assess future Pleistocene discoveries.

"While debate as to a homogeneous or heterogeneous origin for Australian Aborigines is hardly new, recent studies (Thorne in Kirk and Thorne 1976; in Allen *et al.* 1977; Thorne and Wilson 1977) appear to demonstrate a much wider morphometric range in the past. Whether this is to be interpreted as representing separate though related populations (i.e gracile versus robust), or simply extremes of a more highly variable population range remains unclear. However, new material from Western Australia (28—Freedman and Lofgren, in press) confirms that this problem in morphology is not restricted to south-east Australia. Future discoveries and further research are necessary before the situation can be more clearly understood.

"Although their identity remains in doubt, traces exist of their habitation of the new land in the form of stone tools offering some insight into human adaptions to the various Australian environments through time. Yet, in isolation these stone tools are of limited value in understanding the past (e.g. caution expressed in various papers in Wright 1977). These tools were secondary adjuncts to a material culture of which little has been preserved. Indeed, the lithic technology itself is based on ecological and cultural grounds different from those of other areas of the world (Hutterer in Allen *et al.* 1977). Only through taking the stone technology in conjunction with all other available data (food refuse, pollen analysis, site context, etc.) can a truly rounded picture of Australian human prehistory emerge.

"Major studies now completed or under way are beginning to explore this past in Western Australia. In the South-West, Devil's Lair (9) provides the longest continuous occupation sequence as yet studied (Dortch, in press). In the Western Desert, (Puntutjarpa (23) Gould 1977) examines the special circumstances of desert adaptation, while in the Kimberley, Dortch (in Wright 1977) traces human occupation in another environment. A number of other studies examine aspects of Western Australian prehistory (e.g. Clarke and Dortch 1977; Hallam 1972, 1973, 1975, 1977).

"While these studies illustrate what might best be described as a basic unity in economic adaptation for at least the later stages of the prehistoric period considered here, they only hint at those aspects of prehistoric life concerned with the more human quality of day to day living. However, traces of this side of prehistoric life are to be found in a wide variety of rock art that survives today (see Ucko 1977 for a number of Western Australian examples), some of which may eventually be shown to be of considerable antiquity. Finally, it is quite likely that contemporary concepts as to prehistoric human occupation and adaptation are far too rigid in ignoring the significant changes in the prehistoric environment which doubtlessly had direct bearing on daily living, as well as enhancing the very human capacity for social and cultural change."

Discussion and conclusions

If one had to express in just one word the salient characteristic of the whole Western Australian environment at the beginning of the historic period from a human point of view, an appropriate word might be "harsh", "arid" or "difficult". Perhaps the Aboriginal people of the time did not see it this way because they were inheritors of a very long tradition of coping with it. The English invaders certainly did see it so. The exchange in 1838 between the Aboriginal Imbat and the Englishman Grey, reported by Hallam (in Wright 1977) is very illuminating on this subject.

What then would our time traveller, beginning here and taking this excessively comprehensive view, notice as he went back through 200 000 years? If the environment was harsh to begin with, it must have been harsher still from about 10 000 to about 100 000 years ago, forbiddingly so perhaps about 14 000 years ago. During the period of generally high sea levels from about 100 000 to about 130 000 years ago, life might have been a little easier than in the early historic period, but only marginally. Then more difficult conditions would be the norm again almost until the arbitrary beginning of our "prehistoric" period 200 000 years ago. In short, at this level of generalization, the time traveller would register changes only in degree, not in kind, and indeed he might not notice change in kind until he had travelled backward more than 10 000 000 years. The Western Australian environmental stage had been set by middle Tertiary time, and changed only in details subsequently.

But man, like all living things, makes his environmental adjustments to the fine detail, and our time traveller would need to descend from his grand geological perspective in order to make sense of the movements he would see. Thus the Warburton region (23) populated for

the last 10 000 years, might have been truly "desert" previously. The extreme south-west, on the other hand might have involved its sparse human population in unremitting battle with forest, kept at bay only by the skilful use of fire, for most of the last 10 000 years, whereas it might have been more open vegetationally and certainly did support a much greater variety of game, for more than 30 000 years before that. At the latitude of Perth, the coastal, especially riverine, areas might have been relatively densely populated, the jarrah forest practically empty, the wandoo woodland populous and the low woodland occupied, even if only at low density, well to the east of Kalgoorlie for most of the last 10 000 years, perhaps with a shift of population densities towards a coast which was itself continually shifting prior to that.

The separate elements of the environment would be familiar to our hypothetical time traveller, but he would note differences in their relationships to one another, particularly in their spatial relationships, probably most strikingly in those depending on the evanescent boundary separating land from sea. In those prehistoric intervals of particularly rapid rise or fall of sea level, for example the rise between, say, 15 000 and 7 000 years ago, not only the time traveller, but also individual people immersed in the environment, might perceive changes. It may be surmised, for example, that an old man living in the extreme south-west (9) might lament the submergence of rocks or bays from which he used to catch fish as a boy. It is even possible that a percipient person living on the mangrove-lined fringes of the vast savannah that is now the Joseph Bonaparte Gulf (34) might notice encroachment over a few years, since the sea here advanced over 250 km in its 90 m rise in level over this period of about 8 000 years.

The biological component of the environment is an important one, and in fact a case has been made (Goldring 1969) that "environments are essentially the products of biological activity". Even some apparently geomorphological features may be biologically determined, at least in part, as in the case discussed by Rutten (1967) for extensive modification by beavers of northern hemisphere valley forms initially of glacial origin. Man also has his effects, not only on vegetation through his use of fire (Hallam 1975) but in many other ways, for example on the age structure (and hence human food potential) of marine mollusc populations under intensive gathering pressure (Swadling 1976).

Thus our time traveller probably would pay close attention to the biotic environment, and would certainly perceive changes, familiar plant species in unfamiliar places or associations following changes in effective rainfall, or cold-water molluscs in what are now temperate waters, following changes in air and sea surface temperatures, for example. The theme for prehistoric time would be changes in range and local (or total) extinction rather than speciation. For example, Carroll and Galton (1977) suggest that "an essentially modern lizard fauna has existed throughout the Tertiary", and for those two most ubiquitous prehistoric and historic components of the Australian mammal fauna, the macropods and the murids, Archer and Bartholomai (1978) suggest a middle Tertiary explosive radiation and a later Tertiary arrival on the continent respectively, so that both groups were well established and varied before prehistoric time. Their prehistoric record seems to be one of response by established species to environmental changes.

The nature and timing of such responses is best, though still imperfectly, understood for the extreme south-west (Cape Leeuwin-Cape Naturaliste region, 9). Here monotremes are known only from deposits in Mammoth Cave and The Labyrinth, the former known to be and the latter suspected of being beyond the range of radiocarbon dating. Eutherians (murids and bats) seem curiously under-represented in the Mammoth Cave deposit in view of their prominence in younger deposits, and in any case have received little study. Marsupials are therefore the most reliably and comprehensively known group. With these provisos, present knowledge of arrivals and extinctions is outlined in Table 2, and tentative reconstructions of some of the less familiar species given in Figure 2.

Table 2 lists 5 mammal species of about the same body size as the extant western grey kangaroo, or larger, up to *Zygomaturus,* of about the size of a Jersey cow, and at least 8 species of modest size, such as the koala, involved in a first phase of local extinction. It shows incidentally that the currently fashionable piece of jargon "megafauna" not only is unnecessary but misleading, at least in Australia, where few species ever exceeded man greatly in size, and many species of much smaller size have been involved in the "megafaunal" phase of extinction. Yet it does appear to be characteristic of this phase that larger species suffered more than smaller; of those of about human size or larger, only the western grey kangaroo seems to have survived in the extreme south-west. Among the smallest species the murids and bats so greatly outnumber the marsupials and are so poorly known, that no such generalization seems warranted.

A second phase of local extinction may be twofold, with *Sarcophilus* and possibly *Thylacinus* better considered separately from *Perameles, Bettongia lesueur, Lagorchestes, Petrogale, Pseudomys albocinereus, P. occidentalis, Notomys* and *Macroderma.* The latter group make up most of what Baynes *et al.* (1976) call the "non-forest mammals", i.e. species not recorded from the south-western forests in historic time, but known elsewhere from more open or lower plant formations. *Sarcophilus* and *Thylacinus* on the other hand are listed by Baynes *et al.* as "forest mammals" by analogy with their distribution in Tasmania in historic time; not only did they occur widely in plant formations of lower or more open character than our south-western forest, but they also ranged into similar forest. It is suggested that the south-western extinction of *Thylacinus* and perhaps *Sarcophilus* is related to the arrival of *Canis,* whereas the local extinction of *Perameles* and the other non-forest taxa is related to the spread of dense forest at the expense of open plant formations.

Table 2

Arrival, local extinction and survival of mammals in the Cape Leeuwin-Cape Naturaliste region in prehistoric and early historic time.

1. Present in "Mammoth Cave time" (> 37 000 yr B.P.) See Table 1. Man present. (Provisionally, *Zygomaturus*, from Skull Cave, *Zygomaturus, Protemnodon, Sthenurus occidentalis, S. brownei, Vombatus hacketti* and *Phascolarctos* from Devil's Lair, *Macropus (titan?)* from Strong's Cave, and *Zaglossus* from The Labyrinth, are assigned here).
2. First phase of extinction (time unknown, on present evidence likely to be greater than 37 000 yr B.P.). Disappearance of: *Zygomaturus, Protemnodon brehus*, large *?Protemnodon, Sthenurus brownei, S. occidentalis*, "Mammoth Cave wallaby or wallabies", *Thylacoleo, Onychogalea, Vombatus hacketti, Phascolarctos, Zaglossus, Tachyglossus aculeatus* and larger *Tachyglossus* species.
3. Phase of arrivals, covering several thousand years before and after 30 000 yr B.P. *Bettongia penicillata, B. lesueur, Petrogale* and possibly *Lagorchestes, Pseudomys occidentalis* and *Macroderma gigas* make their first appearances.
4. Second phase of extinction. Holocene. Disappearance of: *Sarcophilus, Thylacinus, Perameles, Bettongia lesueur, Lagorchestes* (presumably), *Petrogale, Pseudomys albocinereus, P. occidentalis, Notomys, Macroderma.*
5. Late arrivals: *Canis* (before the local extinction of *Thylacinus;* Merrilees 1979), *Rattus tunneyi* (early Holocene; Porter 1979), *Pseudomys praeconis* (late Pleistocene; Balme *et al.* 1978).
6. Survivals from "Mammoth Cave" to historic time: *Dasyurus, Phascogale, Antechinus, Sminthopsis, Isoodon, *Trichosurus, Pseudocheirus, Potorous, Macropus eugenii, M. irma, M. fuliginosus, Setonix, Pseudomys shortridgei, Rattys fuscipes* and possibly one or more species of bats. (*Absent from the lower layers in Devil's Lair, Balme *et al.* 1978).
7. Survivals from early or middle "Devil's Lair" to historic time, not represented in Mammoth Cave Pleistocene deposits: *Cercartetus, Tarsipes, Bettongia penicillata, Hydromys* and possibly one or more species of bats.

There does not appear to be any other Australian region for which a prehistoric faunistic timetable, even one as loosely framed as Table 2, can be drawn up yet. But it would not be surprising if the Table 2 theme of nett impoverishment were to be established elsewhere, in view of the richness of some known prehistoric faunas (e.g. Kangaroo Island, Hope *et al.* 1977; the Murray River in South Australia, Wakefield in Mulvaney *et al.* 1964; the lower Darling River, Merrilees 1973a) or some which may or may not be prehistoric (e.g. Bingara, New South Wales, Marcus 1976; Gore, Queensland, Bartholomai 1977).

Reasons for the first south-western phase of impoverishment remain obscure. It is not yet clear whether it was exactly or approximately contemporaneous with its counterparts elsewhere in the southern part of the continent, as a climatic interpretation might require. Too little is known of human modifications of vegetation to judge their impact on mammal species of largely unknown ecological characteristics. Practically nothing is known of prehistoric human population densities or subsistence patterns, even whether large mammals were or were not hunted. Hence it seems premature to postulate major effects of human hunting on mammal species of equally unknown population densities.

But it does seem legitimate to infer vegetational diversity from the known mammal diversity in the extreme south-west, even though this cannot yet be checked by pollen or other botanical sequences. Our time traveller would probably notice differences between times of high and low sea level. Continuous forest would accompany high sea levels, and a more diverse vegetational mosaic would accompany low sea levels, possibly to the extent of restricting karri or even jarrah and marri to humid refugia such as dolines or sheltered valleys, while banksia or other open woodland occupied much of what was forested in early historic time. Coastal heath almost certainly would have been much more extensive during low than high sea levels.

This diversity in times of low sea level was such that *Potorous* and *Setonix* could continue to flourish, and *Hydromys* persist for at least some of the time. It seems unlikely, therefore, that extreme aridity could account for the first phase of extinction, and direct or indirect human effects seem more likely.

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Late Quaternary climates of Western Australia: evidence and mechanisms

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Abstract

An attempt is made to provide an outline of the climatic history of Western Australia over a period of the order of 80 000 years, for which some information is available even if sketchy and poorly dated. The late Quaternary was characterised by marked changes in climate, with possibly quite contrasting conditions occurring simultaneously in different parts of Western Australia; the dominant feature, however, was an intensification of aridity. A massive extension of the arid zone coincided with the last global glacial maximum. A consideration of the mechanisms responsible for this event suggests that this was a recurrent theme of the Pleistocene, an interpretation which appears to be supported by the available stratigraphic evidence.

Introduction

In recent years substantial progress has been made in establishing the Quaternary palaeoclimatic history of Australia (see Bowler *et al.* 1976). Unfortunately our knowledge of the Western Australian palaeoclimatic record is sparse when compared to its eastern counterpart. While there exists a large volume of literature which contains reference to Quaternary climatic changes that may have taken place in Western Australia, much of this work suffers from the absence of a satisfactorily-dated framework within which the scattered observations can be placed, and is marred by the tendency of some authors to invoke climatic change as a ready explanation of features which in many cases may be adequately explained by other factors. More recent work, which has been facilitated by both the documented climatic changes that are known to have taken place in other parts of Australia, and the initial results of the Climap project, has shown an explicit concern with the nature and sequence of Quaternary climatic events in Western Australia. It is largely from this work that a framework for understanding the Quaternary climatic and environmental history of Western Australia has begun to emerge.

The aim of this paper is (1) to survey the major evidence that has been advanced by various authors to reflect the Quaternary climatic variations that may have taken place in Western Australia, and from the evidence attempt to develop an outline of the late Quaternary climatic history of Western Australia, (2) to formulate the mechanism of one palaeoclimatic event—widespread aridity—which is likely to have been a recurrent feature of the Quaternary climatic history of Western Australia. As far as possible the evidence is reviewed under separate subject headings, but in places material which is not encompassed by a particular section heading is included to avoid clumsy cross-referencing and repetition between sections. Figure 1 shows the location of many of the sites referred to in the text.

Biotic evidence

Evaluating the climatic implications of faunal and floral remains has been one of the mainstays of Quaternary palaeoclimatic reconstruction. In Western Australia few studies of biotic remains have so far been undertaken with the specific aim of reconstructing the Quaternary climatic history of the area. Especially regrettable is the limited use that has been made of palynology, a technique which in other parts of the world has been fundamental in elucidating the Quaternary environmental history.

Biotic distributions

As probable indicators of Quaternary climatic events in Western Australia, disjunct distributions of flora and fauna have attracted a great deal of attention. Considerable discussion has surrounded the apparent west-east and north-south affinities in the distribution patterns of the Australian flora (Gardner 1942; Specht 1958; Burbidge 1952, 1959, 1960; Gentilli 1961; Green 1964; Marchant 1973; Nelson 1974). A comparison of the vascular floras of south-west and south-east Australia by Green (1964) revealed the existence of several hundred species common in both areas but not in the drier intervening regions. Green considered that some of these populations are true vicariads (defined as closely related allopatric species which have descended from a common ancestral population and attained at least spatial separation) which once occupied continuous areas which became broken by the onset of drier climatic conditions. Some examples include *Lepidosperma angustatum* (south-west), *L. concavum* (south-east); *Casuarina decussata* (south-west), *C. torulosa*

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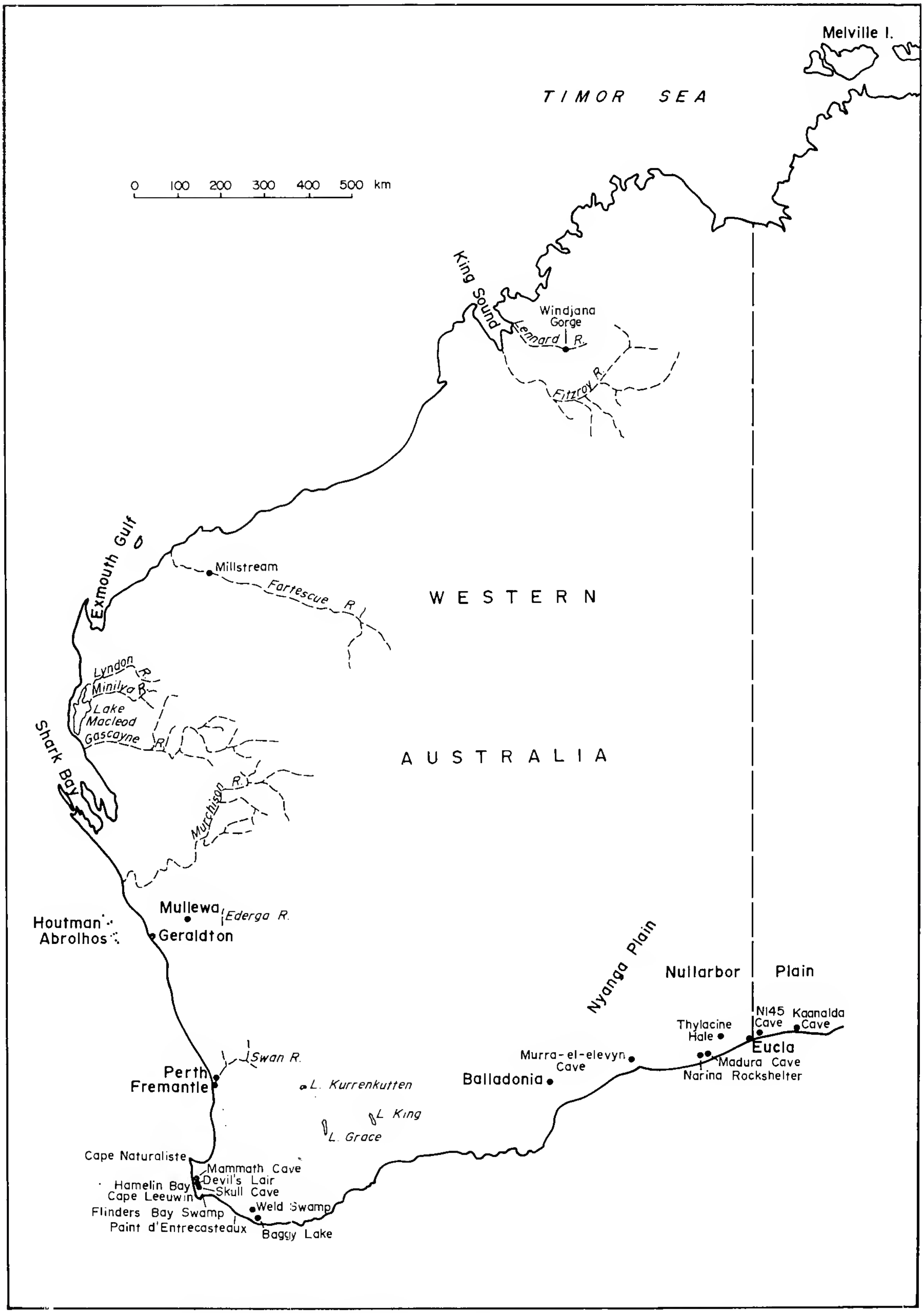

Figure 1.—Location map showing the major sites mentioned in the text.

(south-east); *Acacia leptoneura* (south-west), *A. rigens* (south-east). Estimates as to when this separation of the south-west and south-east flora occurred are widely conflicting, and range from the late Tertiary to the late Quaternary.

North-south affinities in plants are well documented in Western Australia. Gardner (1942) for instance, explained the occurrence in the Geraldton-Perth area of plants common in the Kimberley district, (e.g. *Cartonema, Dioscorea* and *Clematicissus*), as the result of the extension of tropical conditions further south at some time in the past. Other examples include the existence of species of *Terminalia, Owenia, Mallotus* and *Lysiphyllum* in the Pilbara district (Burbidge 1959). The occurrence in tropical areas of isolated species of genera which are well developed in the South-West Botanical Province has been interpreted by several authors as being indicative of the former extension of southern climatic conditions further north (Gardner 1942; Burbidge 1952, 1959, 1960; Gentilli 1961). One species of *Byblis* occurs only in the South-West Province while the only other species in the genus is widespread in the tropical zone. *Verticordia* is mostly confined to the South-West Province and a contiguous semi-arid belt further inland, while in the tropical zone the genus is represented by several species. Other examples include species of *Borya, Persoonia, Boronia, Jacksonia* and *Calytrix* (Burbidge 1960). A relict plant distribution which has not received much attention is the Millstream Palm (*Livistona alfredii*) which is confined to the Fortescue River area at Millstream and a few nearby localities. This species represents the only natural occurrence of palms in Western Australia outside the Kimberley district (Environmental Investigations, Fortescue River 1975).

A number of writers have explained the modern distribution of some amphibians, reptiles, marsupials and birds, east and west of the Nullarbor Plain as the result of greater aridity in the past (e.g. Serventy and Whittell 1976; Main *et al.* 1958; Keast 1961; Kluge 1967). Main *et al.* (1958) explained the existence of frogs with eastern affinities in south-western Australia as the result of successive movements from the primary speciation area in south-eastern Australia across the southern Nullarbor Plain during "pluvial" periods of the Pleistocene. Intervening arid periods were seen as the mechanism of isolation of the eastern and western faunas. Serventy (1951) reached similar conclusions concerning the speciation of the chestnut-shouldered wrens (*Malurus*) which occur throughout the Australian region. Serventy and Whittell (1976) noted numerous examples of the discontinuous occurrence of related avian fauna in Australia. Again the onset of arid conditions during the Pleistocene was invoked to explain these features. Ford (1974), however, has suggested that some isolates of desert species of birds may have formed during relatively wet periods in the Pleistocene.

The only way that the various authors were able to suggest a possible time at which the distributions became separated was by placing them in the context of the palaeoclimatic record available at their time of writing; as the record was often incomplete or in error their conclusions were understandably misleading. This necessity to resort to an existing palaeoclimatic chronology, in order to date a climatic event, postulated on the basis of a disjunct distribution, is a major limitation in the use of disjunct distributions in palaeoclimatic reconstruction. Consequently biotic distributions have been of little value in building up the chronology of Quaternary climatic events in Western Australia, although they have proven useful in indicating likely climatic events that may have taken place.

Nullarbor Plain

Biological evidence for Quaternary climatic changes in the Nullarbor Plain is sparse and often poorly dated. Several workers have suggested that the climate of this region has not changed significantly in the last 20 000 years. Faunal remains found in sediments in Koonalda Cave were dated at approximately 20 000 years BP (Wright 1971, p. 24). Thorne (1971) found no evidence from these faunal remains suggesting an environment different from that of today. Martin (1973) examined pollen from three excavations—N145 Cave near Eucla, Madura Cave and Norina rock shelter. She found that the period 20 000 to about 10 000-8 000 years BP appeared to be more arid than the climate of that area today, with annual rainfall averaging about 180 mm. From about 10 000-8 000 to 5 000-4 000 years BP rainfall apparently increased, and has since maintained an annual average of about 250 mm. The climatic changes indicated by the varying pollen ratios were primarily explained by Martin as being due to the influence of a rising sea level and the consequent climatic effects resulting from a closer proximity to the coast. Martin also suggested that a change in the level of the Aboriginal population at about 4 000-6 000 years BP in the area may have influenced the vegetation patterns.

There is some additional evidence that seems to support Martin's (1973) conclusion that since the middle Holocene the rainfall received by the Nullarbor Plain area has been at the same level as today. The preservation of soft tissue on a *Thylacinus cynocephalus* (Tasmanian tiger) skeleton in Murra-el-elevyn cave (dated at 3 300 years BP, Partridge 1967) and in Thylacine Hole (dated at 4 600 years BP, Lowry and Merrilees 1969) suggested to Lowry and Jennings (1974) that conditions in the caves could not have been much wetter in the intervening time than at present. Ingram (1969) examined the pollen grains found in the desiccated gut of mammalian carcases—*Megaleia rufa* (red kangaroo), *Trichosurus vulpecula* (possum), *Onychogalea lunata* (crescent nail-tail wallaby) and *Canis familiaris dingo* (dingo)—found in Thylacine Hole. These carcases are considered to be between 2 000 and 5 000 years old because they were associated with a *Thylacinus cynocephalus* carcase which has been radiocarbon dated at 4 650 ± 153 years BP, and a *Canis familiaris dingo* carcase which has been dated at 2 200 ± 96 years BP (Lowry and

Merrilees 1969). The fact that the fossil pollen belong to genera common in the present day vegetation, led Ingram (1969) to conclude that the climatic conditions in the area 2 000 to 5 000 years ago, were similar to those of today.

The conclusions of Ingram (1969), Thorne (1971) and Martin (1973) support the view of Jennings (1967), based on the retarded karst development of the Nullarbor Limestone, that there is little evidence for significant climatic changes in the Nullarbor Plain during the Quaternary. In a more recent publication Lowry and Jennings (1974) suggested that there have been changes in the water availability and effective precipitation in the Nullarbor karst during the Quaternary, but that they have never departed substantially in either direction from the present state. They concluded that the karst development on the Nullarbor "may owe much to the cold phases of the Pleistocene when effective precipitation, if not absolute precipitation, was in all probability greater than at present though still low" (Lowry and Jennings 1974, p. 79).

There is some evidence which may support the view of Lowry and Jennings that there was an increase in effective precipitation on the Nullarbor Plain during the Pleistocene glacial periods. Glauert (1912) found the remains of relatively large extinct marsupial species in the Balladonia area, and interpreted them as evidence of a more moist climate at some time during the Pleistocene. Similarly the finding of *Sthenurus* (an extinct large kangaroo) in Madura Cave led Lundelius (1963) to infer more humid conditions in the Pleistocene. These arguments for wetter conditions were based on the assumption that the "giant" marsupials could not have survived in relatively dry habitats. Such an interpretation can be questioned because existing large marsupials in Australia appear to thrive under conditions more harsh than those now prevailing at the fossil sites of the Nullarbor Plain (Lowry and Jennings 1974). However, other evidence which may support Glauert's conclusion, is offered by Richards (1971) who considered that the ancestors of various arthropods found in Nullarbor caves must have colonised that area when conditions were wetter. Furthermore, fossil land snails found in kankar from the Nyanga Plain (the area to the north and west of the Nullarbor Plain) were tentatively compared with the living species *Bothriembryon barretti* by G. Kendrick (in Lowry 1970). While the fossil snails were found within the 150 mm isohyet, Lowry (1970) has found living snails only in areas with more than 250 mm of rainfall. With the absence of absolute dates and reliable stratigraphic information it is not possible to use this evidence to evaluate the suggestion that the climate of the Nullarbor may have been wetter during the glacial periods of the Pleistocene. Nevertheless, the evidence does at least suggest that wetter conditions have occurred.

South-west

Early work on cave deposits in the Cape Leeuwin-Cape Naturaliste region by Glauert (1910, 1914), Lundelius (1960) and others has been revised in a series of papers by Merrilees (1968a, b), Dortch and Merrilees (1972), Baynes *et al.* (1975), Balme *et al.* (1978), Porter (1979) and Merrilees (1979). They report a well-dated continuous sequence beginning before 37 000 years BP (Mammoth Cave), from about 35 000 to 5 000 years BP (Devil's Lair) and from before 8 000 years BP to the present day (Skull Cave), with notes on other less well-dated sites.

It is clear that the region supported a very diverse mammal fauna in the Pleistocene. Some of the species represented in the cave sequences have a wide climatic tolerance (e.g. *Trichosurus vulpecula*—brush-tailed possum); species indicative of drier conditions are also found (e.g. *Bettongia lesueur*—burrowing rat-kangaroo); and remains of species which required rather wet, well-vegetated surroundings are also present in the cave deposits (e.g. *Potorous tridactylus*—long-nosed rat-kangaroo). At some time not yet precisely dated (or perhaps over some considerable period) many large species including *Zygomaturus trilobus* (a diprotodontid) disappeared from the record, and at some time later (late Pleistocene to early Holocene) several of the species most characteristic of drier climates, including *Macroderma gigas* (ghost bat), retracted their ranges out of the region.

The reasons for the disappearance of the large extinct species are still obscure, but Merrilees (1979) suggests that the "dry climate" species were displaced in early Holocene time by the development or extension of dense karri forest like that of early historic time. The implication is that higher effective rainfall, perhaps with less extreme difference between wet and dry seasons, marked the beginning of the Holocene.

An indication of possible Holocene climatic variations in the extreme south-west is given by Churchill (1968), who suggested that rainfall is the major determinant of the distribution of *Eucalyptus marginata*, *E. diversicolor* and *E. calophylla*. Changes in the *E. diversicolor*/*E. calophylla* ratio were thought to provide an index of precipitation changes; a relative increase of the *E. diversicolor*/*E. calophylla* ratio being indicative of wetter conditions. It appears from pollen analyses at Flinders Bay Swamp, Weld Swamp and Boggy Lake that conditions were relatively wetter between 6 000 and 5 000 years BP, followed by a trend towards drier conditions until about 2 500 years BP; after which wetter conditions apparently prevailed until about 1 300 years BP, subsequently it became drier until about 500 years BP. From then to the present there was a trend towards higher rainfall. The similarity of Churchill's findings, that in the south-west conditions were wetter between 6 000 and 5 000 years BP, with the changes recorded in lakes of western Victoria (Dodson 1974a, b) and on Wilson's Promontory, eastern Victoria (Hope 1974) led Bowler *et al.* (1976) to suggest that this constituted a climatic event which affected much of southern Australia. Kendrick (1978) described an assemblage of land snails from palaeosols occurring on and beneath the surface of an elevated ridge of aeolian calcarenite from near Point d'Entrecasteaux. He concluded that the assemblage—*Bothriembryon*

gardneri, *B. consors*, species of *Paralaoma*, *Magilaoma*, *Pernagera*, one other charopid and an undescribed assimineid—suggests a humid, well vegetated, probably forested environment in the Point d'Entrecasteaux area at the time of soil formation, in contrast to the exposed coastal heath that presently characterises the area. Unfortunately the actual age of this assemblage is as yet unknown.

Kendrick (1977) found that fossil molluscs from a mid-Holocene deposit near Guildford have a greater marine affinity than the present assemblage in that area. The fossil deposits have a radiocarbon age of 6 600 ± 120 years BP, coinciding approximately with the Holocene marine transgression. It follows that a greater marine influence would be expected in this part of the Swan River at that time. But despite this, given the present river discharge conditions near Guildford, Kendrick argued that river discharge and seasonality were much lower than at present, which implies that drier climatic conditions prevailed in the Guildford region from at least 6 700 years BP until some time after 4 500 years BP.

Northern areas

Kendrick (1978) has recently described two new species of *Bothriembryon* snails from palaeosols in the Shark Bay district. The two species, *B. douglasi* and *B. ridei*, have no known living descendant in that area. Their extinction at about 80 000 years BP, and the subsequent appearance of camaenid snails (*Rhagada*, *Plectorhagada* and *Angasella* species), as well as the size reduction of *B. costulatus*, are thought to have resulted from the onset of more arid conditions in that area at that time. More humid conditions are thought to have returned to the area since about 10 000 years BP.

Other evidence of Pleistocene climatic events in northern Western Australia comes from Mayr (1944) who discussed the avian faunal exchanges which evidently occurred between Timor and Australia during the period of each Pleistocene glaciation. The fact that most of the recent arrivals from Timor were grassland birds led Mayr to conclude that the climatic conditions prevailing during each glacial were at least as dry or drier than at present. A vertebra from the Ederga River and a tooth from the Gascoyne River district mentioned by Merrilees (1968b, p. 15, the latter tentatively classed as "varanid") may represent crocodilians (D. Merrilees, 1978, pers. comm.), and if so, would imply a possible southward extension of tropical conditions at some time in the Pleistocene.

Gorter and Nicoll (1978) have recently discussed the occurrence, at Windjana Gorge, of indeterminate crocodilian and turtle remains in river gravels of possible Pleistocene age, which may however be as old as early Miocene. The authors claim that the crocodilian remains do not have any important palaeoenvironmental significance. But the presence of remains of the river turtle *Carettochelys* implies a warmer climate than the present one in north-western Australia. However, Gorter and Nicoll stress that without more evidence this conclusion is speculative.

An indication of part of the Holocene climatic history of the northern areas is given by Jennings' (1975) work in the Fitzroy estuary. At present this area experiences a long dry season which in part results in low mangrove forest and mangrove scrub. The stratigraphy of two embayments in the Fitzroy estuary indicates a much wider extent of mangrove swamp at about 7 400-6 000 years BP. In addition the occurrence of fossil stumps of mangrove larger than those of today suggest that tall mangrove forest prevailed at that time. From this, Jennings concluded that at the time a longer and heavier wet season characterised the Fitzroy region. In support of his conclusions Jennings cited Stocker (1971) who suggested that a decline in annual rainfall or a lengthening of the dry season had taken place on Melville Island between 8 000 and 2 000 years BP. Present day jungle fowl on Melville Island inhabit closed communities, particularly monsoon forest. The discovery of ancient mound nests in eucalypt forest led Stocker (1971) to suggest that there has been a gradual decrease in monsoon forest on the island resulting from either a reduction in rainfall or the effects of the Aborigines through their use of fire.

Geomorphological-geological evidence

Longitudinal sand dunes occupy a large area of the Australian continent, but are presently active only in the arid centre. The occurrence of vegetated dunes on the present desert margins, similar in form to their more arid counterparts, provide the most striking evidence of the extension of more arid conditions, at some time in the past. An understanding of the timing and development of these sand dunes, taken in conjunction with the evidence from lake lunettes, has added much to our understanding of Australian Quaternary palaeoclimates (see Bowler (1976) for a review of much of this evidence).

In Western Australia aeolian evidence for a former extension of arid conditions is widespread. Veevers and Wells (1961) described the now stabilised sand dunes and sheets of the Canning Basin, and attributed their development to an arid phase some time in the Pleistocene. Earlier work by Fairbridge (1953) and Brunnschweiler (1957) had already led to the recognition of now stable large aeolian bedforms in this area. Both authors attributed them to the occurrence of extended arid conditions during the Pleistocene. Brunnschweiler (1957) suggested that the inland dunes of the Dampier Peninsula (a term he applied to the area west of King Sound) are continuous with dunes further inland, and proposed that the dunes formed in the Pleistocene during a period corresponding with the Riss Glacial of Europe; however there is no evidence put forward by the author which supports this age estimate. Fairbridge (1953) followed Mayr's (1944) discussion, referred to in an earlier section, and concluded that these dunes stem from a glacial period. In a later work

Fairbridge (1964) compared the way the fixed longitudinal dunes in the Fitzroy area appear to descend below present sea level, as also described by Wright (1964), with an analogous situation in the lower Senegal Valley, and postulated arid conditions and associated dune formation in the Fitzroy area during the last glacial.

The stratigraphic evidence provided by Jennings (1975) confirmed the superficial appearance of the burial of the desert dunes by estuarine fill. A minimum age of 8 000 years BP was inferred from the depth of buried dune sand, while a maximum age of about 140 000 years BP was suggested on the basis of well-presented dune shape. Jennings (1975) related his findings to those of van Andel *et al.* (1967) who interpreted the occurrence of brown calcareous nodules (kankar) in the sediments dated at 17 000 years BP on the Sahul Shelf, as evidence of drier climatic conditions at the last glacial maximum. From this evidence Jennings (1975) reached the conclusion that the most probable time for dune formation in the Fitzroy area was at approximately 20 000 years BP.

Evidence in support of this age estimate for the formation of these dunes comes from the abundance of quartz in Indian Ocean sediments dated at about 18 000 years BP (Kolla and Biscaye 1977). The quartz particles found in these sediments are derived from the adjacent continental area, and the higher amounts of quartz in the sediments suggest increased continental aridity and/or increased intensity of wind at the time of deposition.

Further south in the Exmouth Gulf area at least two inland dune units can be distinguished (Wyrwoll, unpublished). Both appear to predate the Holocene transgression. The older dune unit is capped by a thick indurated calcrete horizon, while on the younger dunes more weakly developed calcareous soils are found. No absolute ages for these dune units are yet available. The presently vegetated dunes of the Gascoyne-Minilya-Lyndon Plain appear to correspond to the younger dunes of the Exmouth Gulf. This dune unit seems to predate the evaporite sequence of Lake Macleod. So far it has not been possible to develop a convincing stratigraphy of the Quaternary sediments of the Exmouth Gulf-Gascoyne area which would time bracket the two dune units with sufficient resolution.

Logan *et al.* (1970) describe two red sand dune units in the Shark Bay region. In the upper part, the older unit (the Peron Sandstone) has a strongly developed nodular calcrete horizon. The Peron Sandstone may correspond to the older dune unit recognised in the Exmouth Gulf area. Although Logan *et al.* provide a comprehensive account of the stratigraphy of the Quaternary sequence of the Shark Bay area, the absolute age of the Peron Sandstone remains uncertain. However, the Peron Sandstone is overlain by the Dampier Transgression, and $^{230}Th/^{234}U$ dating on corals from this transgression is now being undertaken (W. J. E. van de Graaff, 1978, pers. comm.), which will provide at least a minimum age for the Peron Sandstone. The younger dune unit, the Nilemah Sands of Logan *et al.*, consists of unconsolidated red sands which overlie the other Pleistocene formations of this area. This unit corresponds to the unconsolidated dunes of the Gascoyne Plain-Exmouth Gulf region. Degraded inland dune forms can be identified as far south as the Geraldton-Mullewa area (Johnson *et al.* 1954; Wyrwoll unpublished). Further inland Mabbutt (1963a, b) found that an arid event affected the Murchisonia and Salinaland divisions (Jutson 1950), but was unable to determine an age for this event, except to conclude that it took place some time during the Pleistocene. The yellow sands which occur throughout the Perth Basin have been interpreted by Glassford and Killigrew (1976) as a relict aeolian desert sediment derived from sources on the Yilgarn Block and in the Perth Basin. Their conclusion is based on the textural characteristics and mineralogy of the sands, and the occurrence in the sands of kaolin spherites (see Killigrew and Glassford 1976) which they claim have not been observed in marine derived coastal dune or aeolian calcarenite sediments.

In the south Bowler (1976) has dated lunette deposits which fringe Lake Kurrenkutten, Storey's Lake, Lake Grace and Lake King. The results indicate that a short-lived lunette-building event took place between 20 000 and 15 000 years BP, during a period of hydrologic stress; this is an event which has been widely recognised throughout much of southern Australia.

Other geomorphological evidence of Quaternary climatic change in Western Australia is not well documented. The conclusions that Jennings (1967) and Lowry and Jennings (1974) arrived at with respect to the degree of karst development on the Nullarbor Plain have already been noted. Wright (1964) envisaged that the onset of drier climatic conditions in the Pleistocene led to the formation of floodplains along the Fitzroy and Lennard Rivers and their tributaries; and to the extensive alluviation marginal to upland areas in the Fitzroy Basin. Further south in the Geraldton area a "Red Alluvium" unit has been described, and dated at earlier than approximately 40 000 years BP (Wyrwoll 1977). The "Red Alluvium" overlies marine deposits, which on the basis of the molluscan fauna and coastal stratigraphy, were attributed to a last interglacial high sea level, thought to have occurred at about 120 000 years BP (Veeh 1966). At the time of deposition of the "Red Alluvium" streams carried a much coarser bed load than at present, and appear to have had a greater competence and capacity than the present streams. Sediment yields at the time of deposition of the "Red Alluvium" were almost certainly considerably higher than at present. It was tentatively concluded that semi-arid conditions with intense rainfall events occurring more frequently than today, may have prevailed at the time of deposition of the "Red Alluvium".

A fine textured, inset alluvial fill from the Geraldton area, described informally as the "Grey Alluvium" and originally dated at 3 185

± 145 years BP (Wyrwoll 1977) has recently been used by Williams (1978) to support a postulated continent-wide climatic change between approximately 4 000 and 1 500 years BP. In the Southern Tablelands of New South Wales this event may have led to a change in rainfall seasonality, to lower temperatures, and to drier, windier conditions. Since the original date was published an additional ^{14}C date with an age of 1 375 ± 120 years BP (GX-5133), has been obtained for the "Grey Alluvium". The two dates demonstrate the diachronous nature of this alluvial deposit, and question the validity of using the older date as a reliable upper limit for the age of the "Grey Alluvium".

A discussion of the palaeoclimatic significance of palaeosols found in the Tamala Limestone was undertaken by Fairbridge and Teichert (1952). These authors believed that the soil horizons which separate a number of dune generations in the Tamala Limestone indicate minor and short-lived climatic cycles. They claim a change from rendzinas near Hamelin Bay, to terra rossas at the latitude of Fremantle, and travertine crusts along the coast, further north of Houtman Abrolhos. The authors suggest that this gradation of fossil soils confirms their belief that at times during the Pleistocene most of the south-west was subject to more arid conditions.

Limitations of the evidence

Several authors have pointed out the limitations of the various lines of evidence that have been used for Quaternary palaeoclimatic reconstruction in Australia (Jones 1968; Merrilees 1968b; Ride 1968; Calaby 1971; Galloway 1971; Walker 1976, 1978). It has become apparent that palaeoclimatic inferences drawn from plant and animal remains should be made with caution. Walker (1976) has painted a rather grim picture of the present reliability of pollen data for postulating past climatic conditions. In the context of faunal remains and distributions Calaby (1971) has pointed out that homoiothermic and at least the larger poikilothermic animals, have a wide climatic tolerance. The possible role that the Aborigines played in modifying the ecology of the Australian biota (Tindale 1957; Merrilees 1968b; Jones 1968, 1975; Hallam 1975) must also be considered when interpreting biotic evidence in terms of palaeoclimatic events.

Similarly the geomorphological-geological evidence poses considerable problems. The use of alluvial deposits as palaeoclimatic indicators has led to imprecise and often widely conflicting results (see the summary in Flint 1971, p. 306). The reasons why such discouraging results have been obtained can be readily understood when the factors controlling the likely alluvial response to climatic changes are considered, and the equifinality of the problem appreciated (e.g. Schumm 1965; Gessler 1971). Approaching the study of alluvial deposits from the point of view of the palaeohydraulics of the sediments may overcome at least some of the difficulties.

The absence of reliable dates for dune-building phases is also a major stumbling block, although it is hoped that dates from pedogenic carbonate may at least give some indication of the timing of these events. The interpretation of the Perth Basin yellow sand as a relict aeolian desert sediment has been criticised by Lowry (1977), and although some of the criticism has been answered by Glassford and Killigrew (1977), the need for a more comprehensive presentation and discussion of the evidence remains (cf. Clark and Dortch 1977, who also consider the age and origin of the yellow sand).

Chronology of events

The weakness of the available evidence is highlighted when any attempt is made to outline the chronology of the late Quaternary climatic history of Western Australia. The absence of a continuous record, the few absolute dates, and the problems associated with the interpretation of the available evidence, make it impossible to give anything other than a crude and incomplete outline of the late Quaternary climatic history of this area.

80 000-20 000 years BP. Evidence from the central coastal area suggests that in this area the beginning of this period may have seen the onset of arid conditions, which appear to have prevailed until the beginning of the Holocene. The early part of this period saw the frequent occurrence of high precipitation events leading to high sediment yields, and resulting in extensive aggradation in the Geraldton area. The now drier parts of the south may have experienced an increase in effective precipitation during part of this period.

20 000-10 000 years BP. Until about 14 000 years BP intense widespread aridity affected much of Western Australia. The now stabilised and partly degraded dune fields, which in the coastal region extend from the Fitzroy to the Geraldton-Mullewa areas, were formed during this period. The Devil's Lair sequence suggests a significant reduction in the effective precipitation of the lower south-west at the same time. In the south-west and Nullarbor Plain relatively dry conditions seem to have prevailed until the end of the Pleistocene.

10 000 years BP to present. The climatic record for this period as for the earliest period is very incomplete. The onset of the Holocene, with a rising sea level and higher sea surface temperature is likely to have seen a significant increase in precipitation over much of Western Australia. During the period 7 400-6 000 years BP, the north-west appears to have received a higher rainfall which extended further south than at present. More arid conditions may have prevailed in the south-west from 6 700 years BP to about 4 500 years BP. The pollen evidence from the extreme south-west suggests increased precipitation over the period 6 000-5 000 years BP, followed by drier conditions which prevailed until 2 500 years BP.

Mechanism of arid-zone extension

A dominant theme which emerges from the available literature is the apparent expansion of the arid zone, probably at various times during the Quaternary. The most recent widespread expansion appears to be well documented and seems to have coincided with the last glacial maximum (Jennings 1975; Bowler 1976; Wyrwoll and Milton 1976; Kolla and Biscaye 1977). This was an event which in Australia led to an extension of the arid zone along the whole of its present perimeter (Bowler *et al.* 1976); and which can be related to the expansion, at that time, of low latitude arid areas throughout the world (Sarnthein 1978).

Few attempts have been made to interpret this generally accepted expansion of the arid zone in terms of the climatic controls that may have prevailed at that time. One approach that can be taken to obtain an indication of the dynamic palaeoclimatology of past events, is to use the extremes of the present circulation as an analogue for past conditions (see Barry 1975). The assumption inherent in any analogue approach is that the present-day climatic variability includes conditions which were sufficiently frequent in the past to give rise to a substantially different climatic regime (Dzerdzeevski 1963). This amounts to assuming a form of climatic uniformitarianism which, in the light of changing boundary conditions and a possibly almost "intransitive atmosphere"—where the set of equations which represent the behaviour of the atmosphere has a number of solutions, each representing a possible condition of the atmosphere (Lorenz 1976)—is unrealistic. Even over decades, changes of climatic characteristics have been recognised that cannot be attributed to changes in the frequency of a particular circulation pattern, but which arise through changes in the characteristics associated with the circulation (e.g. Perry and Barry 1973). Despite these serious limitations an analogue approach may serve as a useful first approximation to a partial explanation of past climatic events.

The present climate of Western Australia is strongly influenced by the subsiding air of the sub-tropical high pressure belt (STH) (Gentilli 1971, p. 53) which is linked with the descending branch of the low-latitude Hadley cell—the direct cause of much of the widespread aridity of sub-tropical latitudes (Hare 1961). The seasonal displacement of this belt is an important control on both the summer precipitation of the north and the winter rainfall of the southern areas of Western Australia.

The seasonal shifts of the Intertropical Convergence Zone (ITCZ) dominate the dynamic climatology of the northern areas. It is in this zone that the tropical rain-producing disturbances originate (Charney 1968; Bates 1970), so that the location of this feature is fundamental in determining the rainfall of adjacent areas. The location of the ITCZ is linked to the meridional temperature gradient of both hemispheres (Newell 1973), and seems to be determined by low-level convergence in the tropical boundary layer (Charney 1968). Prevailing sea-surface temperatures also seem to play an important role in determining the location of the ITCZ (Charney 1968; Pike 1971). The ITCZ only reaches northern Australia in summer when the STH has been displaced to the south. Associated with the ITCZ is an inflow of moist, unstable air which gives rise to the "Australian summer monsoon". This monsoon circulation however, is shallow and weak, and only a pale imitation of its Asian counterpart.

Despite the fact that during the summer months the STH cells are located far to the south, they can still exert a marked influence on the precipitation of the northern areas. Intense anticyclones situated over the Australian Bight can give rise to a quite stable atmosphere above the Pilbara heat low, and through this prevent the incursion of monsoonal depressions and disturbances into the northern areas (Rutherford and Hannan 1956; Falls 1970).

A comparison between the rainfall received by northern Australia in February 1952, and February 1953, highlights the control that the STH exerts on the rainfall of the northern areas. In February 1952, when northern Australia was in the middle of its worst drought in 60 years, the highs migrated 5° closer to the equator than normal. In February 1953, however, when rainfall was high the track of the migrating highs lay up to 10° poleward of normal (Ramage 1971, p. 273).

The winter rainfall of the southern area of Western Australia is largely associated with moist unstable westerly winds and with the associated troughs in this westerly airstream. The mean depression track and the associated zone of maximum rainfall are situated off the south-west coast, and this accounts for the decreasing precipitation gradient northward (Wright 1974). Pittock (1973, 1975) has demonstrated a correlation between the latitude of the STH and the amount of precipitation received by the south-west. This correlation has been substantiated by Wright (1974) whose work focuses on the south-west of Western Australia. These authors have shown that a more southerly location of the STH can significantly reduce the winter rainfall received by the south-west.

Using the present climatic regime as an analogue for past conditions it is evident that an increase in anticyclonicity would directly result in widespread aridity over much of Western Australia. Wyrwoll and Milton (1976) have argued that the lowering of the mean July sea and land surface temperatures (Climap 1976; Gates 1976a, b) would have thermally intensified the anticyclone. The resultant anticyclone would have combined the high pressure qualities of both anticyclonic types—warm and cold (Wexler 1951)—and therefore would have been extremely intense (also see Derbyshire 1971). Under these conditions the frequency of breakdown of anticyclonic cells would have been considerably lower, and with the consequent development of blocking conditions, winter rainfall would have been confined to the extreme south-west of Western Australia.

To describe the synoptic conditions governing the summer months during full glacial periods it was envisaged (Wyrwoll and Milton 1976) that anticyclonic conditions would have weakened, but possibly only to the extent that conditions were more similar to those of the present day late spring or early autumn. This would imply that during the full glacial summer the STH was located significantly further north than during the present summer months. From the present day situation it is clear that this would have been a very effective mechanism in reducing the rainfall received by the northern areas.

A northward displacement of the STH during glacial summers is supported by the so called "Z" criterion developed by Smagorinsky (1963), and subsequently used by Flohn (1964, 1965) for locating the position of the STH. The "Z" criterion takes the form

$$\cot \phi = -\frac{a}{h} \frac{\partial \ln \theta_{PE}/\partial y}{\partial \ln \theta_{PE}/\partial z} \qquad (1)$$

where ϕ is the latitude of the STH, h a scale height of the atmosphere of about 9 km, which approximates the height of the 500 mb surface, and a is the radius of the earth, θ_{PE} is the partial potential equivalent temperature (see Appendix 1), and z and y are the vertical and horizontal axes respectively. Instead of using the potential equivalent temperature Flohn (1965) has approximated equation (1) by using the potential temperature (θ) and by relating this to the actual temperature, Flohn has prepared a nomogram from which the effect of changes in the meridional and vertical temperature gradients on the position of the STH can be read (Fig. 2).

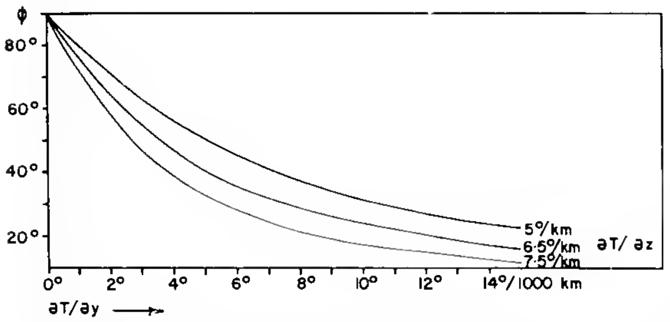

Figure 2.—Location of the subtropical high pressure cell (ϕ) as a function of the meridional and vertical temperature gradients (after Flohn 1965).

The validity of the "Z" criterion appears to have been established by Korff and Flohn (1969) who demonstrated a close relationship between the monthly mean equator-pole potential temperature gradient—which they took as a crude approximation for $\partial \theta_{PE}/\partial y$—and the position of the STH. Further support was offered by Pittock (1973), who found that equation (1) fairly accurately predicts the monthly mean latitude of the STH over Australia. However, Greenhut (1977) has recently developed a new criterion for locating the STH which predicts an opposite response to changes in $\partial \theta_{PE}/\partial y$ and $\partial \theta_{PE}/\partial z$ to those predicted by the "Z" criterion. It is difficult to reconcile the prediction of this new criterion with the success met by Korff and Flohn and Pittock when using the "Z" criterion. These two studies would appear to suggest that the adoption of the "Z" criterion is a valid first approximation despite Greenhut's conclusions.

During glacial periods the overall meridional temperature gradient of the upper troposphere may have been similar or even less than that of today (Kraus 1973; Williams 1978). However, it is likely that a strengthened meridional temperature gradient occurred in the middle troposphere over the mid-latitudes. According to Korff and Flohn these are the latitudes which determine the location of the STH. From Figure 2 it is evident that an increase in the mid-latitude meridional temperature gradient would be further enhanced if an increase in the vertical temperature gradient had taken place. For equatorial areas Kraus (1973) suggested that during glacial conditions a three-fold amplification of the changes in sea surface temperature occurred by the time the ascending air reached the upper troposphere. This occurred as the result of a decrease in latent heat release, and would only be significant over areas with a sea surface temperature greater than approximately 20°C. In addition there is some evidence from South-East Asia (Verstappen 1975) and New Mexico (Wright *et al.* 1973) that during full glacial conditions a lapse rate of temperature with height greater than present, may have prevailed at least in the lower latitudes. The combined evidence suggests that an equatorward displacement of the STH during full glacial conditions would have been highly likely.

A northward displacement of the STH should result in a concomitant displacement of the ITCZ and the depressions associated with it. Available evidence (Bryson 1974; Beer *et al.* 1977) suggests that the amount of northward displacement of the STH would be amplified, possibly up to three times, with respect to the ITCZ. Evidently an equatorward displacement of the STH would be very effective in causing the extension of arid conditions in the northern areas.

In addition, because of the high contribution that tropical cyclones make to the annual precipitation of the north-west (Milton 1978), widespread aridity in that area during the last glacial maximum implies an absence of tropical cyclones at that time. Whether this was due to an absence of cyclogenesis as a result of reduced sea surface temperatures (Webster and Streten 1972) or simply a more westerly seaward path is not possible to establish. As tropical cyclones are very effective converters of potential to kinetic energy, and play an important role in the general circulation of the atmosphere (Landsberg 1960), a possible absence of tropical cyclones during full glacial periods would have important repercussions on the general circulation.

An equatorward displacement of the STH during full glacial stages has also recently been suggested by Rognon and Williams (1977) and appears to be supported by the available geomorphological evidence. The orientation of

clay lunettes in southern Australia suggests that the summer anticyclone over Australia in full glacial times was positioned some 5° further north than today (Bowler 1976). In addition Bowler envisaged a strengthening of the westerly air flow over southern Australia at that time. In Western Australia the geomorphological evidence of dune and lunette orientation appears to support this reconstruction. But this circulation pattern is fundamentally different from that required by Glassford and Killigrew (1976) to account for the derivation of the Perth Basin yellow sand. Their interpretation implies that surface easterlies prevailing as far south as the Leeuwin Block, occurred with sufficient frequency and intensity to transport large volumes of sand westward. This, taken in conjunction with the proposed extension of desert conditions to the coast, could only occur under a circulation pattern in which the STH during a large part of the winter, is located further south than its present summer location. From equation (1) it follows that this could only occur during periods in which a substantial increase in $\partial\theta_{PE}/\partial z$ and/or a decrease in $\partial\theta_{PE}/\partial y$ had taken place. While it would seem that such an extreme southward displacement of the winter STH is unlikely, if it did occur it would almost certainly have occurred during interglacial stages.

During the present interglacial the maximum southward displacement of the STH should have occurred at the "climatic optimum" (approximately 6 000 years BP) when increased global temperatures and higher atmospheric moisture content may have significantly reduced $\partial\theta_{PE}/\partial y$ and/or increased $\partial\theta_{PE}/\partial z$. From the previous discussion of the present precipitation controls, it follows that if the STH was displaced southward at approximately 6 000 years BP, climatic conditions more arid than at present should have occurred in the south-west of Western Australia at that time. Kendrick's (1977) conclusions seem to support this idea, but this is rather scant evidence in view of the earlier work by Churchill (1968), and the discussion of the Australian mid-Holocene climatic evidence by Bowler *et al.* (1976). However, if it is valid that the location of the STH is as important a control of rainfall in Western Australia as has been suggested, then there is an additional way in which the idea that there was a significant southward displacement of the STH at about 6 000 years BP can be tested, and Kendrick's conclusions at least partially checked. It follows that if a significant southward displacement of the STH took place at that time, and that this displacement also characterised the circulation of the summer months, higher summer rainfall extending further south can be expected in the northern areas at that time. Jennings' (1975) conclusion, that during the period 7 400-6 000 years BP a heavier wet season characterised the Fitzroy region, may lend some support for the idea outlined above.

If it is tentatively concluded that during interglacial stages, a significant southward displacement of the STH can occur, which may lead to more arid conditions in some parts of the southwest, it remains to be shown whether during previous interglacial stages, this southward displacement could have been extreme enough to lead to an extension of arid conditions as far south as the Leeuwin Block. The suggestion that such a massive southward extension of arid conditions may have occurred during a past interglacial stage is certainly difficult to reconcile with what is thought to happen in low-latitude arid areas during interglacial stages (see Sarnthein 1978). In addition aridity extending as far as the coast in a western littoral during a period in which sea surface temperatures were higher than at present is difficult to visualise.

Doubts remain whether it is really necessary to invoke a significant displacement of the STH to account for the aridity of the northern areas during full glacial conditions. Manabe and Hahn (1977) showed that tropical continental aridity at glacial maximum is closely related to stronger surface outflow (or weaker inflow) over tropical areas. This resulted from the hydrostatic response to the greater reduction of surface temperatures over continents than oceans and the increased albedo value that characterised tropical areas at that time. Increased albedo values over sub-tropical areas are important in leading to the extension of arid conditions. Increasing the albedo of a surface contributes to a net loss of radiative heat thereby creating a horizontal atmospheric temperature gradient with respect to the surrounding areas. Through this a circulation is set up which transfers heat aloft and maintains thermal equilibrium through sinking and adiabatic compression (Charney 1975). In sub-tropical areas this subsidence is superimposed on the descending branch of the Hadley Cell, clearly accentuating its effect. The positive feedback relationship which is set up as the result of increased albedo values almost implies that "the desert feeds upon itself" (Charney 1975).

A number of other considerations also point to the fact that during full glacial conditions much of Western Australia must have been much drier than today. Analyses of Indian Ocean cores (Vella *et al.* 1975; Williams and Johnson 1975; Bé and Duplessy 1976) show that during the last full glacial an equatorward shift of the Australian-Subantarctic front and the Sub-Tropical Convergence zone took place, with the result that much lower sea surface temperatures characterised the ocean off Western Australia. Microfaunal and oxygen isotope analysis of core RC9-150 (Bé and Duplessy 1976), taken from the continental slope 125 km north-west of Perth, showed that mean summer sea surface temperatures at 18 000 year BP were up to 6C° lower than those of today.

Sea surface temperatures exert an important control on precipitation (e.g. Namias 1975; Wright 1977), and in tropical areas show a strong correlation with storm frequencies (Wendland 1977). Today the presence of warm water off the coast in winter makes south-western Australia far wetter than any corresponding western littoral (Gentilli 1952, 1971; Lydolph 1957). An examination of the rainfall distribution of the dry western littorals of the various continents (Lydolph 1957), revealed that except

for Western Australia the annual rainfall increases inland from the driest area which lies in a narrow coastal strip. This extreme aridity in the immediate coastal belt may be explained by the stabilising effect of a cold offshore current, which today is largely absent off the coast of Western Australia (Wooster and Reid 1963). In the Indian Ocean the low-latitude ocean circulation is strongly determined by the trade winds (Knauss 1963). With an increase in the strength of the trades during full glacial periods, which now seems likely in the light of evidence from different parts of the world (e.g. Parkin 1974; Molina-Cruz 1977) a cold offshore current along the coast of Western Australia can be expected. In any event with the considerably lower sea surface temperatures, that the deep-sea core evidence suggests, a tendency towards aridity should have been pronounced. This conclusion was in part anticipated by Brooks (in Mayr 1944) over 30 years ago. He suggested that during full glacial conditions a cold current was present off the west coast of Australia, which he suggested would only be a winter-time phenomenon. The presence of this current "would have had the effect of extending the winter-time high pressure area and contributing at this season to the aridity of the west coast of Australia" (Mayr 1944, p. 129).

The existence of arid conditions over parts of Western Australia during full glacial periods would have been further facilitated by the exposed continental shelves of those periods. That the increased continentality would result in an appreciable reduction in the precipitation received by the north-west was again pointed out by Brooks, and more recently reiterated by Nix and Kalma (1972). The important control that this mechanism is likely to have had on the late Quaternary climates of the Nullarbor Plain (Martin 1973; Martin and Peterson 1978) was noted in an earlier section.

Summary

Despite the sketchy nature of the evidence it is now apparent that Western Australia experienced widespread climatic changes over the last 80 000 years. Of these changes the most severe was clearly the arid phase which characterised part of the closing 10 000 years of the Pleistocene. Arid-zone extension, coinciding with the global glacial maxima, must have been a recurrent feature of the Pleistocene climatic history of Western Australia. This inference is in part supported by the stratigraphy of the Quaternary sediments of the Shark Bay-Exmouth Gulf area. But it needs to be borne in mind that aridity in Australia finds its origin in the late Tertiary (see Bowler 1976), so that the Pleistocene extensions of the arid zone are the culmination of a trend which started some 10 million years ago. The extreme arid phases of the Pleistocene must have deeply influenced the lives of the original human inhabitants of this part of the continent, and their effect on both flora and fauna was equally profound. Similarly much of the physical landscape still bears the imprint of these phases.

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Appendix 1

The partial equivalent potential temperature is given by

$$\theta_{PE} = K\theta \qquad [A1]$$

where θ is the potential temperature. If air at pressure p and temperature T is brought adiabatically to a standard pressure P_0 of 1 000 mb., its temperature θ at that standard pressure is known as its potential temperature. This is given by

$$\theta = T(P_0/P)^{\kappa} \qquad [A2]$$

$\kappa = (c_p - c_v)/c_p = 0.288$ for dry air

c_p is the specific heat at constant pressure

c_v is the specific heat at constant volume

In equation [A1] the function K introduces the modification in the potential temperature due to the presence of moisture in the air; for details of this see Greenhut (1977).

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Contents

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